EFECTOS DE LA ESCALA Y LOS GRADIENTES AMBIENTALES EN LA DIVERSIDAD DE BRIÓFITOS EPÍFITOS DE LOS BOSQUES DE QUERCÍNEAS IBÉRICOS

Tesis doctoral presentada por Nagore García Medina

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Dirigida por los doctores Francisco Lara García,
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El director El director El director

El doctorando

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Eskerrik asko

Índice general

Resumen

La diversidad depende de una serie de factores interrelacionados que operan a través de diferentes escalas. Estudiar dichos factores y relacionarlos con los procesos subyacentes es un tema central tanto para la Ecología como para la Biogeografía. El objetivo principal de este trabajo consiste en identificar los factores que mejor explican la diversidad, y determinar cómo interactúan a través de las escalas. Para ello, se han empleado los briófitos epífitos como organismos modelo, ya que debido a sus características biológicas y al sustrato relativamente inerte en el que habitan, están ligados estrechamente a las condiciones ambientales tanto locales como regionales. Esto los convierte en organismos especialmente adecuados para el estudio de los factores a varias escalas. El trabajo descansa sobre un marco conceptual basado en la idea de que existe un conjunto –o *pool*– de especies que tienen el potencial de colonizar una localidad determinada mediante procesos de dispersión y en tiempo ecológico. Estas especies van pasando a través de filtros de distinto tipo que operan a distintas escalas espacio-temporales (filtros evolutivos a gran escala, filtros ambientales a meso-escala y filtros bióticos a pequeña escala), hasta configurar la diversidad observada.

La aplicación de un protocolo de selección de localidades, basado en un algoritmo *p*-median que maximiza la cobertura ambiental y geográfica, ha permitido capturar un porcentaje elevado de la variabilidad ambiental y geográfica de los bosques seleccionados. Además, se ha constatado la importancia de hacer comprobaciones sobre la variabilidad (geográfica y ambiental) y la diversidad cubiertas, de modo que se pueda optimizar el esfuerzo de muestreo y garantizar la calidad de la información obtenida. El éxito del protocolo de selección se ha visto reflejado en el alto número de especies y novedades encontrado. En total se han censado 89 especies de briófitos epífitos, y se ha contribuido a ampliar el conocimiento de la distribución de numerosos briófitos, con más de 70 novedades provinciales.

En cuanto al estudio de los patrones de diversidad, los resultados obtenidos muestran la idoneidad del marco conceptual adoptado y, por consiguiente, la importancia de las relaciones jerárquicas de arriba abajo para la estructuración de las comunidades. En este sentido destaca el papel primordial del *pool* de especies en la estructuración de las comunidades, que queda reflejada tanto en los patrones de riqueza como en la influencia de las regiones en la estructuración de las comunidades a pequeña escala.

Además, los resultados indican que en lugar de ser contrapuestos, los procesos de nicho y neutro representan extremos de un mismo gradiente. El balance entre ambos depende de varios factores, entre los cuales destaca la escala a la que ocurren

los procesos ecológicos que afectan al grupo estudiado. Así, a escala de paisaje la diversidad de briófitos epífitos depende principalmente de los gradientes ambientales, que incluyen tanto las condiciones climáticas (principalmente precipitación, temperatura y la interacción entre ambas), como de las características hábitat. Por contra, a medida que disminuye la escala los factores asociados a procesos neutros van ganando importancia. A la menor de las escalas la importancia de los procesos neutros es, en términos generales, mayor, aunque está sujeta a cierta variabilidad. Así pues, a la menor de las escalas los procesos neutros llegan a ser dominantes, sobre todo en la Región Atlántica donde las condiciones climáticas son más favorables para el desarrollo de briófitos epífitos.

Adicionalmente, se proponen una serie de modificaciones del marco conceptual general. Por un lado, el hecho de que los procesos dispersivos sean más importantes a la menor de las escalas indica la importancia que pueden tener las dinámicas de ocupación a esta escala, por lo que es necesario incorporar este tipo de procesos de forma explícita en los marcos conceptuales. Además, algunas de las variables medidas a la menor de las escalas resultaron ser relevantes para explicar tanto la riqueza como la composición específica. Esto da idea de la importancia de los patrones emergentes, y llama a incorporar a los estudios macroecológicos relaciones de abajo hacia arriba que vinculen directamente las variables a pequeña escala con la diversidad a mayores escalas.

Abstract

Biodiversity patterns depend on a number of interrelated factors operating through different scales. Studying these factors and trying to unveil the underlying processes is a central issue for both Ecology and Biogeography. The main objective of this work is thus to identify the factors that best explain local diversity, and determine how they interact across scales. We use epiphytic bryophytes as model organisms for their suitability to the study of factors at various scales. Due to their biological characteristics and the relatively inert substrate on which they thrive, they are responsive to local as well as to regional environmental conditions. The work is based on a conceptual framework that relies on the concept of species pool: the set of species that have the potential to colonize a given locality by dispersal processes in ecological time. According to the adopted conceptual framework, the species pool is successively filtered through different types of filters operating at different spatial and temporal scales (large-scale evolutionary filters, meso-scale environmental and biotic small-scale filters).

The application of selection methodology based on a *p*-median algorithm that maximizes the captured environmental and geographical distances allowed covering a high percentage of the environmental and geographical variability of the study area. Besides, we have verified the importance of assessing the covered variability and the obtained diversity in order to optimize the sampling effort. The high number of species and novelties recorded reflects the success of the applied protocol. Overall, we registered 89 species of epiphytic bryophytes and contributed to widen the knowledge on the distribution ranges of several bryophytes, with more than 70 provincial novelties.

Regarding the study of diversity patterns, our results evidence the benefits of adopting this conceptual framework and thus, the importance of the hierarchic top-down relationships. In this sense, the size of the species pool stands out as a primary factor structuring communities. This importance can be seen both in the analysis of richness patterns as well as in the influence of the identified regions to structure communities at the smallest scale.

Additionally, we have also shown that, rather than competing, neutral and niche processes represent extremes of the same gradient. The balance between these two kinds of processes depends on several factors, among which the scale at which ecologically relevant processes occur outstands. At the largest scale considered, landscape-scale diversity of epiphytic bryophytes mainly depends on environmental gradients including the climatic conditions (mostly precipitation, temperature and the interaction among them) as well as the characteristics of forest

structure. However, when scale decreases, factors associated with neutral processes gain importance in general terms, but also show some variability. Hence, at the smallest scale, neutral processes become dominant, especially in the most favorable areas.

Furthermore, we suggest some modifications to the general conceptual framework. On the one hand, the fact that the dispersal processes are more important at the smallest scale indicates the potential importance of occupancy dynamics at this scale, calling for explicitly incorporating them into the conceptual framework we use. In addition, some of the variables measured at the smallest scale were found to be relevant to explain both richness and species composition. This gives an idea of the importance of emerging patterns, and calls for incorporating bottom-up relationships that link directly the small-scale variables and diversity at larger scales.

CHAPTER

1

Introducción, objetivos y estructura de la memoria

Introducción

Los estudios que conforman la presente memoria de tesis doctoral giran en torno a una idea principal: encontrar las causas que condicionan la diversidad y la identidad de las especies de briófitos epífitos que alberga un árbol en un bosque determinado y, al mismo tiempo, averiguar de qué dependen los cambios en la riqueza y la composición específica de un bosque a otro. Expresada en términos más generales, la pregunta que nos planteamos indaga dos cuestiones que han intrigado durante mucho tiempo a ecólogos y biogeógrafos: ¿de qué depende la variación espacial de la biodiversidad?; y ¿cómo se relacionan dichas variaciones a pequeña y gran escala?

El desarrollo de respuestas que integren todos los factores que determinan los patrones de diversidad se ha visto dificultado por la complejidad de los procesos implicados y las múltiples escalas a considerar (Nogués-Bravo 2003). Durante décadas, desde los ámbitos de la Ecología y de la Biogeografía se han desarrollado líneas de trabajo que divergían profundamente en sus planteamientos. Desde la perspectiva de la Ecología la mayor parte de los esfuerzos se han centrado en aproximaciones experimentales y escalas espaciales relativamente pequeñas (Fig. 1.1), que abarcan desde la diversidad local a la regional (Jenkins & Ricklefs 2011). El objetivo ha sido, principalmente, relacionar las condiciones ambientales locales y las interacciones entre especies con la variación de la diversidad (Nogués-Bravo 2003; Jenkins & Ricklefs 2011). Por el contrario, desde la óptica de la Biogeografía la mayoría de los trabajos han empleado un enfoque más analítico, dirigido a desentrañar el efecto de los procesos históricos y evolutivos a escalas mucho mayores (Fig. 1.1). Afortunadamente, en la última década se está produciendo un progresivo acercamiento conceptual que está facilitando reconciliar ambos enfoques (Villalobos & Paknia 2011).

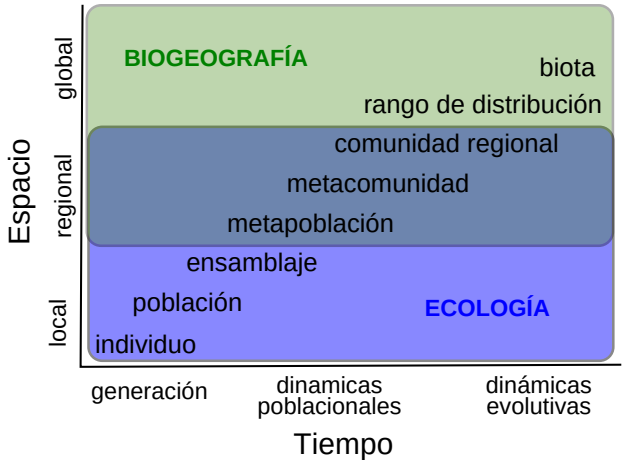

Figura 1.1: Escalas espacio-temporales que abarcan la Ecología y la Biogeografía. Adaptado de Jenkins & Ricklefs (2011)

El acercamiento entre ambas disciplinas se ha vertebrado en torno a una serie de debates conceptuales, entre los cuales destaca el modo de entender las comunidades. Desde la Ecología se interpretaban las comunidades como sistemas saturados de especies, en los que la selección del ambiente y, en todo caso, las interacciones bióticas eran las causas principales de la diversidad observada (Jenkins & Ricklefs 2011). Esta premisa asume de manera implícita que la dispersión no constituye un limitante a la coexistencia de especies, al menos a las escalas en las que se hacían habitualmente los trabajos en Ecología. En este sentido, el desarrollo primero de la teoría de biogeografía de islas (MacArthur & Wilson 1967), y recientemente de la teoría neutra (Hubbell 2001), han puesto de manifiesto la importancia de la dispersión sobre la estructuración de las comunidades a escala local. La teoría de la biogeografía de islas colocó a las comunidades locales en un contexto regional. Posteriormente, la teoría neutra extendió los planteamientos de la teoría de biogeografía de islas incorporando la idea de la estocasticidad, mediada por los procesos dispersivos en las comunidades locales, como motor principal –en realidad único– de la estructuración de las comunidades, al menos dentro de un grupo trófico. A esto se ha sumado la constatación de la importancia de los factores regionales sobre las comunidades locales (Ricklefs 1987, 2007), que ha ganado fuerza en los últimos decenios. En conjunto, se ha pasado de entender las comunidades como sistemas saturados en especies, y por tanto cerrados a la influencia regional, a reconocer la importancia de los procesos dispersivos, tanto regionales como locales, en la estructuración de las mismas.

Otro de los factores que ha influido de forma determinante en la integración de las perspectivas ecológica y biogeográfica ha sido el reconocimiento de la escala como parte importante de la investigación sobre los patrones de diversidad (Wiens 1989; Levin 1992). Por un lado, la adquisición de datos es un proceso ligado a la escala, pues la mayor parte de las variables pueden tomarse con mucho detalle sólo en unas pocas localidades o, a menor resolución, en áreas más extensas (la excepción la proporcionarían los avances en medición remota por satélite). Pero aún más importante es el hecho de que los patrones medidos a determinada escala no tienen por qué mantenerse a escalas mayores o menores. Los efectos de la escala sobre la diversidad se mencionan ya en trabajos de principios del siglo XX (ver Schneider 2001). Sin embargo, inicialmente se consideraba un problema que era necesario eludir, mientras que a partir de la segunda mitad del siglo XX ha habido un cambio en la interpretación de su importancia, de modo que la escala se considera ahora un factor relevante que debe ser cuantificado y cuyo efecto es necesario comprender (Wiens 1989; Levin 1992; Whittaker, Willis & Field 2001).

Asociado al desarrollo de estos conceptos, se ha generado un marco conceptual que considera de forma explícita la jerarquía de escalas y procesos implicados, y que reconoce tanto la importancia de los procesos históricos y dispersivos como la de los procesos ecológicos, tales como los filtros ambientales o las interacciones bióticas (Whittaker *et al.* 2001; Rajaniemi *et al.* 2006; Guisan & Rahbek 2011). Los estudios integrados en esta memoria de tesis doctoral descansan sobre la base conceptual de dicho marco. En él se parte de la idea de que existe un conjunto –o *pool*- de especies que tienen el potencial de colonizar, mediante procesos de dispersión y en tiempo ecológico, una localidad determinada (Fig. 1.2). Estas especies van pasando a través de filtros de distinto tipo que operan a distintas escalas espacio-temporales (filtros evolutivos a gran escala, filtros ambientales a meso-escala y filtros bióticos a pequeña escala), hasta configurar la diversidad observada (Rajaniemi *et al.* 2006; Guisan & Rahbek 2011; Sydenham *et al.* 2015).

A nivel práctico, incluir todos estos factores de forma conjunta, teniendo en cuenta varias escalas simultáneamente, presenta importantes dificultades. Por un lado, la cantidad de factores implicados es muy elevada y, además, sus interrelaciones son complejas. Por otro, los efectos de algunos de los factores (i.e. dispersión, evolución) son difíciles tanto de observar como de analizar experimentalmente. Además, la naturaleza de las relaciones a diferentes escalas varía en función de las características ecológicas y funcionales de los organismos. Por ello, es necesario acumular un número significativo de estudios en organismos muy diversos para poder realizar generalizaciones válidas sobre las relaciones a través de las escalas.

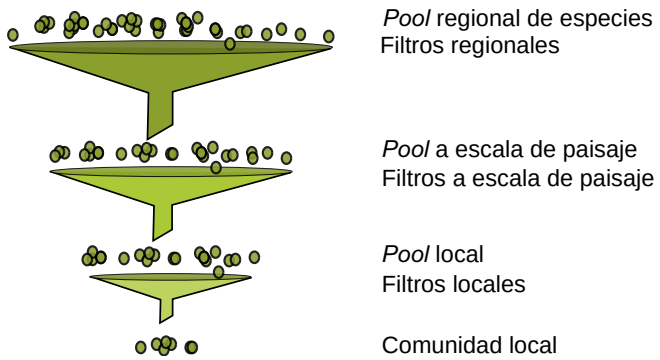

Figura 1.2: Esquema de la jerarquía de filtros a diferentes escalas

Una de las líneas que es importante desarrollar para avanzar en el estudio de los factores a diferentes escalas consiste en estudiar desde una perspectiva ecológica los patrones de diversidad a escalas intermedias, ya que es a este nivel donde se encuentran los procesos a escalas regional y local (Harrison & Cornell 2008; Jenkins & Ricklefs 2011). Sin embargo, esta aproximación no está exenta de limitaciones siendo posiblemente la más importante la de tratar de identificar los procesos subyacentes mediante la observación de patrones. Aunque es cierto que los patrones de diversidad no tienen necesariamente que reflejar directamente los procesos que los originan, también lo es que los procesos dejan huellas que se pueden intentar asociar a unos u otros patrones de forma diferencial. Así, el estudio de las distintas hipótesis y de los patrones que se asocian con mayor probabilidad a cada una de ellas puede contribuir, como mínimo, a descartar las hipótesis menos plausibles y, en el mejor de los casos, a identificar las causas más verosímiles (Shipley 2000; Vellend *et al.* 2014). Un buen ejemplo proviene del estudio de la relación entre riqueza local y regional, donde se asumía que las comunidades no saturadas de especies darían lugar a relaciones lineales entre ambas medidas (Srivastava 1999). Aunque actualmente se reconoce que el patrón lineal puede verse afectado por otros procesos (ver por ejemplo He *et al.* 2005; Damschen & Brudvig 2012), el estudio de la relación entre riqueza local y regional ha dado lugar a un debate muy fructífero, que ha contribuido de forma significativa a poner en duda la asunción de que las comunidades están saturadas de especies.

Los briófitos tienen una serie de características que los convierten en buenos organismos modelo para explorar la estructuración de patrones y procesos a múltiples escalas. Por un lado su pequeño tamaño, su simplicidad anatómica y su incapacidad para regular el estado de hidratación interno hacen que tengan una vinculación muy directa con el ambiente circundante (Moe & Botnen 2000; Pharo & Zartman

2007). Además, también son buenos indicadores de las condiciones ambientales a mesoescala (Lara 1993; Albertos 2001; Gignac 2001; Medina *et al.* 2010), por lo que representan un buen sistema de estudio en el que detectar filtros ambientales a diferentes escalas.

De entre los sustratos colonizados por los briófitos, el ambiente epifítico representa un hábitat especialmente adecuado para el estudio de los patrones a diferentes escalas. La corteza de los árboles es un sustrato relativamente inerte, que apenas amortigua las condiciones ambientales, que retiene bajas cantidades de agua, y que está sujeta a importantes variaciones en la temperatura (Barkman 1958). Por todo ello, los epífitos se desarrollan bajo condiciones más intensamente ligadas al clima que los organismos que crecen sobre otros sustratos (Benzing 1998). En este sentido, el ambiente epifítico representa un sistema de estudio relativamente simple en el que el efecto de los factores meso y microclimáticos pueden observarse con mayor nitidez. Además, la estructuración jerárquica y anidada de árboles y bosques también contribuye a simplificar, en cierta medida, la delimitación de las escalas relevantes para el estudio de la diversidad de los briófitos epífitos. Así, los árboles representan islas en un ambiente poco favorable, el interior del bosque, y los bosques representan a su vez islas enclavadas en un paisaje desfavorable para el desarrollo de epífitos.

Más allá de su papel como organismos modelo, investigar la diversidad de briófitos es un ejercicio relevante en sí mismo. Su estudio permite profundizar en el conocimiento de un grupo relativamente poco explorado en este sentido. Buena parte del debate acerca de los factores que determinan la diversidad de briófitos se ha centrado en desentrañar la importancia relativa de los factores abióticos a diferentes escalas. En este contexto, los resultados de los diferentes estudios enfocados en estas plantas son bastante divergentes. Mientras que algunos autores han destacado la mayor importancia del mesoclima (Zechmeister *et al.* 2003; Pharo *et al.* 2005; Callaghan & Ashton 2008), otros han encontrado que el microclima tiene un papel preponderante (Vitt, Li & Belland 1995; Humphrey *et al.* 2002; Vanderpoorten & Engels 2003; Bacaro *et al.* 2008; de Oliveira *et al.* 2009; Hespanhol *et al.* 2011). Si bien algunos trabajos han considerado más de una escala (de Oliveira *et al.* 2009; Hespanhol *et al.* 2011; Király *et al.* 2013), la gran mayoría atienden a solo una, por lo que es muy posible que la inconsistencia en los resultados esté influida por las diferencias en la escala y la extensión de los distintos estudios. Además, el enfoque actual está centrado en la importancia relativa de los factores, pero dado

que es muy posible que lo que sucede en una escala afecte a las demás es necesario realizar estudios que incluyan la interacción entre los factores que inciden a pequeña escala y los factores mesoambientales.

Objetivos

El objetivo general de los estudios realizados en el marco de esta tesis doctoral es identificar los factores que mejor explican la diversidad de briófitos epífitos, y determinar cómo interactúan a través de las escalas. Esta cuestión tan amplia se aborda de manera más concreta gracias a la definición de los siguientes objetivos específicos:

- Diseñar una estrategia de muestreo que recoja los gradientes ambientales y geográficos del área de estudio de forma sistemática y garantice disponer de datos de calidad para el estudio de las variaciones geográficas en briófitos epífitos.

- Ampliar el conocimiento sobre los briófitos epífitos en la Península Ibérica, intentando paliar las lagunas que los posibles sesgos en el muestreo han podido ocasionar en la zona de estudio.

- Estudiar en profundidad la relación entre los filtros ambientales y bióticos a diferentes escalas, y la riqueza, la composición específica y la abundancia de los briófitos epífitos.

- Analizar la transmisión de efectos a través de las escalas y evaluar el impacto de los factores que operan a escalas intermedias sobre la diversidad a pequeña escala.

- Desarrollar un marco conceptual jerárquico que considere los factores a diferentes escalas y sus interacciones al estudio de la diversidad de briófitos epífitos.

Para ello se han estudiado los patrones de riqueza, composición y abundancia de especies de briófitos epífitos sobre bosques dominados por *Quercus ilex, Q, faginea* y *Q. pirenaica* a tres escalas diferentes: árbol, parcela y bosque. El área de estudio escogida se sitúa principalmente en las porciones españolas de las cuencas del Duero y el Tajo, por lo que abarca un gradiente ambiental y geográfico amplio. Cada uno de los capítulos trata de responder a uno o más de los objetivos planteados.

Estructura de la memoria

El Capítulo 2 supone la primera aproximación al estudio de la diversidad de briófitos epífitos de esta memoria. Con el estudio que recoge se pretendía identificar y desentrañar la estructura los principales factores abióticos que influyen sobre la diversidad de briófitos epífitos. Para ello se emplearon datos de un trabajo previo realizado en el NW de la Península Ibérica (Albertos *et al.* 2001). Se contaba con un número limitado de variables a pequeña escala y una descripción climática precisa de las localidades de muestreo.

Los resultados de este capítulo dan una idea de la complejidad de las relaciones consideradas y nos empujaron a plantear la necesidad de analizar más en profundidad las relaciones entre el mesoambiente, el microambiente y la diversidad a distintas escalas. Para ello, se decidió ampliar el área de estudio extendiendo el gradiente ambiental (Capítulo 3), al mismo tiempo que se aumentaba el número de medidas relacionadas con las condiciones de hábitat y microambientales (descritas en el Capítulo 4).

La ampliación del área inicial de estudio planteó la problemática de la selección de puntos de muestreo. Para solventar la cuestión se diseñó un proceso de selección que tuviera en cuenta de forma explícita tanto el conocimiento previo de la brioflora epífita como los gradientes ambientales y geográficos imperantes en el espacio geográfico considerado. El método de selección de las localidades y los principales resultados del proceso se describen en el Capítulo 3. A continuación, en cada uno de los bosques seleccionados para el estudio se realizó un muestreo exhaustivo de las comunidades briológicas y las condiciones ambientales, a tres escalas diferentes: bosque, parcela y árbol. En el Capítulo 4 se describe pormenorizadamente el diseño de muestreo y las medidas tomadas y se presenta la base de datos en la que se basa el resto de capítulos.

El Capítulo 5 supone la primera aproximación a los resultados de dicho muestreo: se presentan las especies encontradas y su relevancia para el conocimiento de la distribución de los briófitos ibéricos.

Finalmente, los Capítulos 6 y 7 tratan de desentrañar los efectos de los factores abióticos, a través de las escalas, sobre la riqueza y la beta diversidad, respectivamente, de los briófitos epífitos en el área estudiada. En ambos capítulos se explora la intensidad de los factores ambientales en las distintas escalas y la transmisión de efectos a través de las mismas.

Todos estos capítulos han sido publicados o preparados para publicar en diferentes revistas especializadas. A continuación se indican las referencias de los

trabajos que corresponden a cada capítulo:

Capítulo 2 Medina, N.G., B. Albertos, F. Lara, V. Mazimpaka, R. Garilleti, D. Draper & J. Hortal. 2014. Species richness of epiphytic bryophytes: drivers across scales on the edge of the Mediterranean. *Ecography*, **37**, 80–93.

Capítulo 3 Medina, N.G., Lara, F., Mazimpaka, V. & Hortal, J. (2013) Designing bryophyte surveys for an optimal coverage of diversity gradients. *Biodiversity and Conservation*, **22**, 3121–3139.

Capítulo 4 Medina, N.G., Lara, F., Mazimpaka, V., Albertos B., Alonso I. & Hortal, J. bryophytes of *Quercus* forests in Central and North inland Iberian Peninsula. *Frontiers of Biogeography*, **7**, (en prensa)

Capítulo 5 Medina, N.G., Mazimpaka, V. Hortal, J. & Lara, F. Catálogo de los briófitos epífitos que crecen en bosques de quercíneas del cuadrante noroccidental ibérico. *Boletín de la Sociedad Española de Briología*, **45-46**, (en prensa).

Capítulo 6 Medina, N.G., Bowker M., Hortal J., Mazimpaka V. & Lara F. Shifts in the importance of species pools and environmental controls of epiphytic bryophyte richness across multiple scales. *Ecography* (enviado)

Capítulo 7 Medina, N.G., Calatayud J., Lara F., Draper I., Mazimpaka V. & Hortal J. Biogeographically distinct regions show different patterns of across scale environmental filtering. (listo para enviar)

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CHAPTER

2

Species richness of epiphytic bryophytes drivers across scales on the edge of the Mediterranean

Abstract Spatial variation in species richness is one of the most frequently studied topics on macroecology. However, the relative importance of the factors affecting richness across scales and their influence on some groups of small-sized organisms, such as bryophytes, remain unclear. We evaluate the relative importance of biogeographic region, climate, topography, forest structure and abundance in shaping epiphytic bryophyte richness at both local (forest) and sample (trunk) scale on the boundary between the Atlantic and Mediterranean regions in NW Spain. For that purpose we used simple, multiple and partial regressions, hierarchical partitioning and partial least squares path analyses. Although climatic variables related to water availability during spring and summer were the most important predictors of bryophyte richness, their effects were moderated by winter temperature. Abundance, in contrast, was mostly related to forest structure. Biogeographic region was not significantly related to richness. Interestingly, forest richness was the best predictor of trunk richness. Our results highlight the importance of seasonal distribution of rainfall and temperatures and support that the richness of bryophyte communities is constrained by mesoscale climatic factors, in particular the interplay between water and energy availability. In contrast, abundance seems to be controlled by habitat characteristics. We also detected a strong top-down structure between both scales of measurement evidencing a scaling down of the climatic effect: richness at the sample scale is controlled mainly by local richness and local richness is in turn controlled by climate, so mesoscale climatic gradients are indirectly limiting richness at the smallest scale.

2.1 Introduction

Species richness is perhaps the most studied aspect of biodiversity. Despite this, the factors and mechanisms behind richness gradients, and how they vary across scales and between different groups, are still under debate (e.g. Mittelbach *et al.* 2007, Ricklefs 2007, Swenson 2011). This is the case of bryophytes, a unique group within land plants in many aspects. They are, in general, two orders of magnitude smaller than vascular plants (Tuba *et al.* 2011) and lack the mechanisms to effectively control their water uptake or loss (e.g. Proctor 2009). Due to these characteristics, bryophyte communities are commonly thought to be strongly dependent on local factors and microclimate (Moe & Botnen 2000, Ingerpuu *et al.* 2003, González-Mancebo *et al.* 2004, Löbel, Dengler & Hobohm 2006, Pharo & Zartman 2007, Cole *et al.* 2008, Mota de Oliveira *et al.* 2009).

The diversity of bryophyte communities is not only determined by local factors and small-scale processes. Rather, it also varies as a response to phenomena acting at larger scales, among which climate is generally recognized as a major determinant of both the geographic distribution of bryophyte species and the diversity of their communities (e.g. Gignac 2001, Pharo *et al.* 2005, Callaghan & Ashton 2008). However, the actual importance of climate for bryophyte richness remains elusive; while some studies have found this factor to be the primary determinant of bryophyte richness (Zechmeister *et al.* 2003, Pharo *et al.* 2005, Callaghan & Ashton 2008), others identified a major role of local and landscape characteristics (Vitt *et al.* 1995, Humphrey *et al.* 2002, Moser *et al.* 2002, Vanderpoorten & Engels 2003, Bacaro *et al.* 2008). Such differences may be related to the particular characteristics of each bryophyte guild (Raabe *et al.*, 2010), but other factors such as the scale of analyis or the intensity of the climatic gradient may be influencing the observed divergence. There is a growing body of research on the effects of climate, local factors and microclimate on bryophyte richness and it is known that different factors affect diversity patterns at different scales (see e.g. Rydin 2009). However, a general understanding of the combined effects of these factors is yet lacking and to date no study has investigated whether the relative effects of the abovementioned factors scale down from the local to the small scale.

Epiphytes grow under more demanding climate-based constraints than terrestrial plants (Benzing 1998). Their dependence on the atmospheric supply of both water and nutrients make them good indicators for habitat characterization and floristic zonation (Frahm 2002, Lara & Mazimpaka 1998, Draper *et al.* 2006). Here we study the bryophytes inhabiting oak trunks in forests dominated by *Quercus robur*

L. and *Q. pyrenaica* Willd. in the Northwest of the Iberian Peninsula, within an area placed on the boundary between the Atlantic and Mediterranean regions. The complex topography of this area results in strong changes in temperature and water balance within a few kilometers, creating a complex mosaic of communities as species from both regions intermingle. On each forest we measured the richness of epiphytic bryophytes at local and sample scales (i.e. the species present in each forest and on each tree trunk, respectively).

In this work we investigate the link between mesoscale (climate, topography, and forest structure) and small scale (phorophyte characteristics) factors, and the richness and abundance of bryophytes at the two scales of analysis (local and sample scales). To do so, first we define the relationships among environmental factors, species richness and abundance at the local scale (objective 1). Within this objective (1a) we analyze the importance of both seasonal and annual averages of climatic variables and (1b) we evaluate the relative importance of the most meaningful climatic variables and a range of other factors (including topography, forest structure, or local abundance, among others) on the diversity of epiphytes at the local scale. Given the strong climatic gradient found in the studied area, we expect climate to have a significant role in explaining richness at the local scale.

Then we explore how all these factors are related with bryophyte diversity at the two scales of analysis simultaneously (objective 2).

We formulate a conceptual model relating the effects of the whole set of factors throughout the two scales of analysis (Fig. 2.1). Within this model (2a) we study the correlates of abundance at local (forest) and sample (trunk) scales. Here, intense competition for space is expected to reduce richness at high surface cover (see e.g. Grace 1999), while facilitation would increase richness at high cover creating a positive linear relationship (Bergamini 2001), since competition for space occurs at the smallest scale, if abundance is relevant for richness, its effect should be detectable mainly at the trunk scale. Also, (2b) we evaluate how local richness and climate are related to richness at the sample scale. We hypothesize that if small scale interactions are weak, the number of species in the local pool will be important and the correlation between richness at the two scales (local and sample) will be strong (i.e. regional enrichment; see e.g. Ricklefs 2000, White & Hurlbert 2010), and as a consequence the effect of climate will scale down from the local to the sample scale. On the contrary, if small scale interactions are strong, local richness will be less important and bryophyte richness at the forest scale will be weakly correlated to richness at the sample scale.

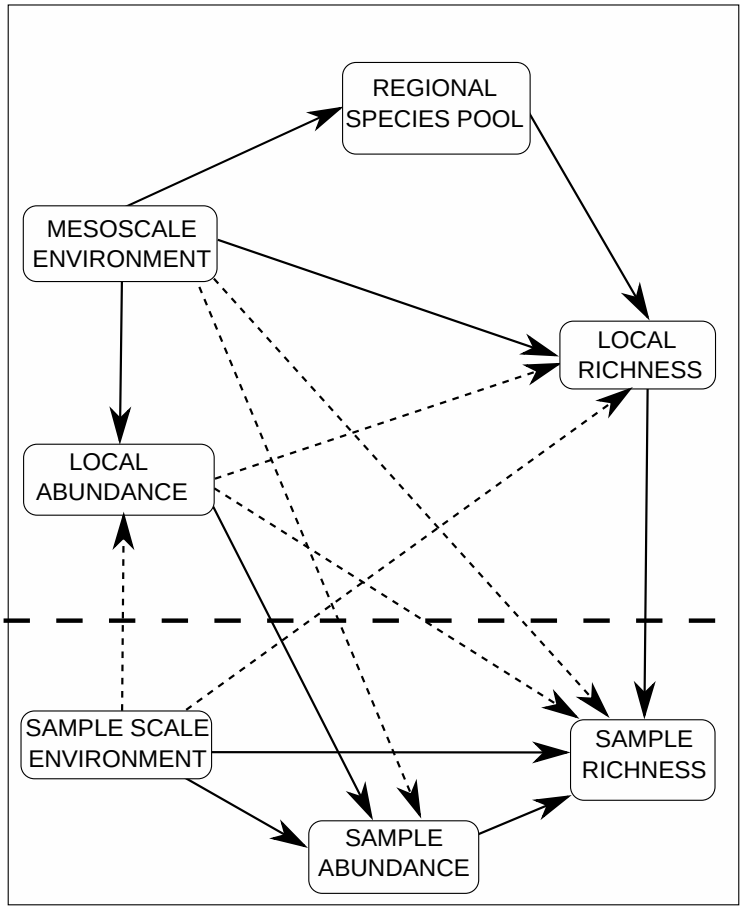

Figure 2.1: Conceptual model of the hypothesis about the relationships between bryophyte diversity and abundance at several scales, and environmental predictors. Lines (dashed and solid) indicate tested hypotheses and arrows hypothesized direction of causality. Dashed lines indicate paths expected to be non significant and solid lines paths expected to be significant. Local scale refers to forest scale while sample scale refers to tree scale

2.2 Methods

Study area

The study was carried out in Northwestern Iberian Peninsula, approximately between 42° 50'-43° 0' N and 6°30'-7°50' W (Fig. 2.2). In this area, elevation ranges from 240 m a.s.l. in the localities near the northwestern coast to 2,185 m a.s.l. in the Cantabrian Mountains. The complex topography includes a number of mountain ranges mainly in SW-NE direction, dissected by numerous valleys of diverse orientations. This results in a series of pronounced climatic gradients that run perpendicular to

the predominant directions of the mountain ranges. The northwest of the study area pertains to the Atlantic domain and is characterized by a longer humid period (some localities receive more than 3,000 mm of precipitation per year). In contrast, the southeastern area is under Mediterranean influence, with a considerably longer summer drought period and more extreme temperatures. Despite these differences in the extremes of the gradient, the complex topography produces a wide and irregular transitional zone rather than a clear boundary between areas of Atlantic and Mediterranean climate (Baselga & Novoa 2005). A hundred sampling sites were set up to sample thoroughly such transition zone, and eleven additional sites were located in the peripheral Atlantic area. These latter sites are used as markers, since they had a clearly defined Atlantic climate regime, also enlarging the spectrum of climatic conditions covered by the survey.

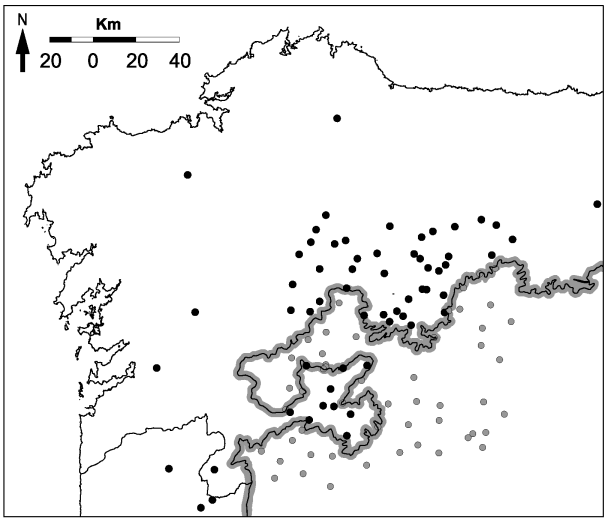

Figure 2.2: Location of the study area in the Northwestern Iberian Peninsula. Grey points indicate the surveyed forests within the Mediterranean region while black points represent surveyed forests within the Atlantic region. Grey line indicates the limit between Atlantic and Mediterranean regions sensu Rivas-Martinez (1987)

Data collection

Epiphytic mosses were sampled in 111 forests dominated by *Quercus pyrenaica* and/or *Quercus robur*. The presence of other phorophytes was rather rare. We therefore collected samples only on trees of *Q. pyrenaica* and *Q. robur*. Both tree species hybridize frequently in the area, making difficult to ascribe the samples to

one species or the other. We performed a preliminary study on phorophyte specificity in a forest from the study area, to ascertain whether there were differences between the bryophyte communities growing on the tree trunk of each of these species. In this study we found no differences in bryophyte composition or richness between both tree species (Albertos *et al.* 2001). Sampling sites were selected trying to make forest characteristics as homogeneous as possible, by choosing forests with similar conservation status, and discarding those with canopy clearing, or located in the vicinity of roads or in very narrow valleys (see Albertos *et al.* 2005 for details). At each sampling site, 20 healthy upright trees with diameters between 15 and 45 cm and more than 5% bryophyte cover on the trunk were selected by a team of 3 or 4 researchers, who walked in different directions. Size of forest patches and number of trees with bryophyte cover was uneven, so the area of each forest covered by the survey was variable (although never larger than 1 km^2). For a reduced number of forests either a sample was damaged or it was not possible to find twenty healthy trees of the required characteristics, which resulted in a total of 2206 sampled trunks (instead of 2220). Samples were taken from 400 cm^2 quadrats (20 x 20 cm), in the side of the tree with the highest bryophyte cover, at a trunk height between 1.50 and 1.80 m above ground. All bryophytes included in the quadrat were collected and analyzed in the laboratory. Percentage of bryophyte cover in the quadrat was estimated before sample removal.

Three different measures of richness were extracted from these data, one describing the diversity at the trunk (i.e. sample) scale, and two at the forest (i.e. local) one. (1) *Species richness per trunk* was measured as the number of species found in each plot (n=2206); it accounts for species richness at the sample scale and its variations are thought to reflect processes related to microenvironmental factors and biotic interactions. (2) *Average forest richness*, calculated as the mean species number over all the samples in each forest (n=111), is a measure of local species richness; in this case, the effect of individual trees is smoothed, so it is expected that variations in this metric are more related to mesoscale environmental variables. (3) *Overall forest richness*, measured as the total number of species found in each forest (n=111), represents species richness at the local scale; thus, it may be affected by variations in sample richness, but also by species turnover within the forest, so it is expected to be dependent on both habitat heterogeneity and mesoscale environmental gradients. Two measures of abundance were calculated to account for its variation at the two scales of measurement: (4) *Abundance per trunk* (i.e. sample abundance) as the percent of bryophyte cover in each sample

(n=2206); and (5) *Average abundance* (i.e. local abundance) as the mean percentage of bryophyte cover in each forest (n=111).

Environmental and regional predictors

Environment was described according to five groups of predictors that correspond to different types of factors:

(1) *Phorophyte characteristics* were described by two variables measured in the field: exposure at which the sample was taken (North, South, East or West) and tree diameter at breast height.

(2) *Forest structure* was accounted for through the mean and variance of tree diameter in each forest (measured in the field) plus the level of forest development extracted from the Spanish forestry map (Ruiz de la Torre 1990), which gives a qualitative estimate for each forest patch, coded as an ordinal variable ranging from 5 to 8 in the studied forests (5= bushy forest, 6=tall and dense forest, 7=tall dense forest with a rich bush layer, 8=tall dense forest, canopy formed by several species).

(3) *Climatic characteristics* were obtained from a GIS database based on data from the network of meteorological stations of the Spanish National Institute of Meteorology (INM 1992) and the Portuguese National Institute of Meteorology and Geophysics (SMN 1961-1970, INMG 1971-1990). Climatic variables were selected after Tuhkanen (1980). All climatic variables used in this study were interpolated through Kriging with External Drift (Goovaerts 1997), using elevation as an auxiliary variable. In total, 27 climatic descriptors including seasonal temperatures and rainfall and seasonality indexes were analyzed. All climatic variables were obtained at 1km^2 resolution and processed in a GIS program (Clark Labs 2006).

(4) *Topography* is described through three variables. The general aspect of each forest was recorded in the field and later transformed into a binary variable, distinguishing shaded (North and East facing slopes) or sunny exposure (South and West facing slopes). Altitude above the sea level was measured in the field using a GPS and topographic maps. Slope was calculated *a posteriori* from a digital elevation model (Hijmans *et al.* 2005) of 1km^2 resolution.

(5) *Biogeographic region* was accounted for by categorizing each forest according to the biogeographic region (either Atlantic or Mediterranean, a binary variable) it pertains to (Fig. 2.2). We used a widely accepted bioclimatic classification of Spain (Rivas Martínez & Gandullo 1987) to delimit the Atlantic and Mediterranean regions. This classification has proved to be a good predictor of the changes in communities of small organisms at the sample scale (see Guil *et*

al. 2009). It is available at fine-grain resolution and is a reasonable proxy to the zonations defined for bryophytes in the area (Albertos 2001). In fact, the bryofloristic composition of the trunks diverges largely between the different zones defined by this classification in the study area. Briefly, Atlantic bryoepiphytic assemblages are characterized by the dominance of pleurocarpous mosses, mainly *Hypnum andoi* A.J.E. Sm. and *H. cupressiforme* Hedw., and the abundance of several liverworts, such as *Metzgeria furcata* (L.) Dumort, *Frullania fragilifolia* (Taylor) Gottsche, Lindenb. and Nees and *F. tamarisci* (L.) Dumort. Conversely, Mediterranean forests are dominated by acrocarpous mosses with species of the genus *Orthotrichum* being the most frequent (in particular *O. affine* Schrad. ex Brid. and *O. rupestre* Schleich. ex Schwägr) (Albertos 2001, Albertos *et al.* 2005). Since some of the forests were close to the border between both regions (Fig. 2.2), we identified the sampling points falling within a 4 km buffer around this border, and tested if there was any effect of the biogeographic region by comparing the results obtained using all sampling points with those coming from all points except those within the buffer. As there were no significant differences between both analyses (not shown), we only show the results of the regional classification without taking into account the buffer.

Additionally, we evaluated the possibility of an influence of the amount of habitat available in the landscape on local richness, but the proportion of oak forest within 5 km around each survey point was not correlated to either average or overall forest richness (not shown).

Statistical analyses

2.2.0.1 Effect of mesoscale climatic gradients over richness at the local scale

The effects of the climatic predictors on local scale community descriptors (overall forest richness, average forest richness and average abundance) were analyzed using an array of regression-based analyses. Environmental variables are often collinear (Legendre & Legendre 1998), which could compromise the selection of variables in multiple regression analyses. In order to avoid multicollinearity problems during the selection procedure, the variables to be included in the model were selected in a two-step analysis (see e.g. Hortal, García-Pereira & García-Barros 2004, Hortal *et al.* 2008). We regressed the predictors one by one against each one of the three dependent variables, ordering them according to their goodness-of-fit. At this step we searched for quadratic relationships, including a quadratic term in each of the individual regressions and performing a forward selection that

compares the AIC of the alternative models while penalizing the increase in the number of predictors (stepAIC function in MASS package). Only the models that retained both the quadratic and linear terms of the predictor after the forward selection were retained as quadratic. Also, we constructed a correlation matrix between all considered predictors, selecting the one with the higher explained variability, and subsequently removing all predictors that were highly correlated (Pearson r >0.8) with it. Thereafter the variable with the higher explained variability from the remaining ones was selected. This process was repeated until all predictors with a significant relationship with the dependent variable were evaluated, rendering three groups of preselected independent variables (one per dependent variable). More than 20 variables were evaluated in the first step (see Table A1, supplementary material) but a maximum of seven per group of predictors were retained for the next steps of the selection procedure.

On the second step, we used the small sample size-corrected Akaike index (AICc) to select the most parsimonious model in a tradeoff between complexity and information. All possible models were compared by means of their partial Akaike weighting (see Burnham & Anderson 2002, Diniz-Filho, Rangel & Bini 2008). In order to account for uncertainty in model selection we examined the profile of ranked AICc weightings (Fig. A2) of all the candidate models. Additionally, we calculated the importance of the variables computed as the sum of the relative evidence weights of all models in which the term appears (Fig. A3). The results show that the selected model correctly identifies the most important terms.

Both the quadratic term and the variable alone were added to the models for the variables that presented a significant hump-shaped relationship with the explanatory variable. However, none of the quadratic terms was retained in the final models. We also searched for first order interaction terms. To do this, we first mean-centered all the variables, and then calculated all possible models including combinations of pairwise interactions between the main effects. When including an interaction term the corresponding main effects were always included (Calcagno & Mazancourt 2010). AICc values were calculated for all models and the model with the lowest AICc was retained for each dependent variable. To ensure that multicolinearity of the models was low, we checked variation inflation factors (VIF) of the variables entering the model; when the VIF of any pair of predictors was larger than 5, the variable with the smallest explanatory power was removed and the second step of the selection procedure was run again. This was repeated until VIF of all variables in the final models were at acceptable levels (VIF<5). Spatial autocorrelation of the residuals was analyzed using Moran's I coefficient at 12

different distance classes. The absence of significant levels of spatial autocorrelation in the residuals would indicate that all spatial structure in the data is explained by the included variables (Diniz-Filho, Bini & Hawkins 2003). Residuals of the resulting models were also surveyed in order to detect departures from normality and heterocedasticity and to identify outliers. Richness measures were square-root transformed in order to improve normality in final residuals. Finally, we analyzed influential points by means of Cook's distance; no data point had a distance larger than 1 so all of them were retained. Model comparisons were carried out using SAM 4.0 (Rangel, Diniz-Filho & Bini 2010), interaction analysis using the R package glmulti (Calcagno & Mazancourt 2010) and all other analyses were done with the basic packages in R (R Development Core Team 2009) and our own scripts.

To evaluate the relative importance of the explanatory variables, we performed a hierarchical partitioning on the subsets of variables selected in the final best models. To do so we used the hier.part package in R (Mac Nally 2000, Mac Nally 2002). Briefly, this analysis splits the variation explained by each predictor into independent and joint effects, allowing assessing the importance of the common effect among variables, and thus accounting for their collinearity.

Then we evaluated the contribution of climate, biogeographic region, topography and forest structure in explaining richness variability. To estimate how much of richness variance can be attributed to each set of variables we performed a partial regression analysis (Borcard, Legendre & Drapeau 1992, Legendre 1993, Legendre & Legendre 1998). Briefly, each variable pertaining to a factor (for example, altitude within topography factor), is regressed against the rest of the variables in the remaining factors (altitude vs. the variables in forest structure, altitude vs. the variables in climate and altitude vs. region). Then each variable within a factor is regressed against all the possible combinations among factors (altitude vs. the variables within forest structure plus the variables within climate and region). The residuals of this regressions are retained. Finally, richness is modeled using these residuals as predictors. Coefficients of determination of the partial regression provide all the information required to calculate the magnitude of the independent effects and the interaction among factors (see full description and examples at, Lobo, Castro & Moreno 2001, Hawkins, Porter & Diniz-Filho 2003, Hortal *et al.* 2008). All partial regression analyses were performed with vegan package (Oksanen *et al.* 2011) in R (R Development Core Team 2009).

Analysis of the relationships among factors within and between scales

To study the effects of the whole set of factors at the two scales of analysis we performed a partial least squares path analysis (PLSPA). This type of analysis is a soft approach to structural equation modelling with fewer distribution assumptions (Tenenhaus *et al.* 2005). This technique allows handling multiple dependent and independent variables in such a way that some variables act at the same time as predictor and as dependent variables. In PLSPA, standard errors and significance of the coefficients are calculated through bootstrapping, which avoids making assumptions about the distributional properties of the variables (Tenenhaus *et al.* 2005). We first designed a general model that reflects the causal paths we wanted to test (Fig. 2.1). Then we developed the measurement model by including the actually measured predictors (Fig. 2.3).

The model comprises three categories of environmental variables (Table 2.1). (1) Biogeographic region, consisting of one latent variable related to one indicator. (2) Mesoscale environment, made up of three subcategories: (2.1) climate, comprised of the climatic variables selected in the regression model (Table 2.2). As the relationships between climatic variables and richness turned out to be very complex, adding them in raw form could compromise the performance of the PLSPA. To simplify this set of relationships, we reduced the dimensionality of the climatic variables by means of a principal component analysis (PCA) and included as indicators the first two axes of the PCA (Table A3), supplementary material), (2.2) topography (two latent variables, three indicators) and (2.3) forest structure (two latent variables, three indicators). (3) Small scale environment, a latent variable related to two indicators, tree diameter and sample exposure. First we constructed the saturated PLSPA model where all the paths were included irrespective of our expectations (Fig. 2.3). Then we sequentially eliminated the non significant paths until the model included only significant paths. The results shown correspond to the model with the remaining significant paths. These analyses were done using SmartPLS (Ringle, Wende & Will 2005).

2.3 Results

We found 76 epiphytic bryophyte species within the study area. At the local scale overall forest richness ranged from 5 to 26 species (see Fig. A1, supplementary material), average forest richness from 2.5 to 8.8 species, and average abundance varied between 11.6% and 95.7% bryophyte cover. At the sample scale, richness per trunk ranged from 1 to 17 species and abundance per trunk varied between 5%

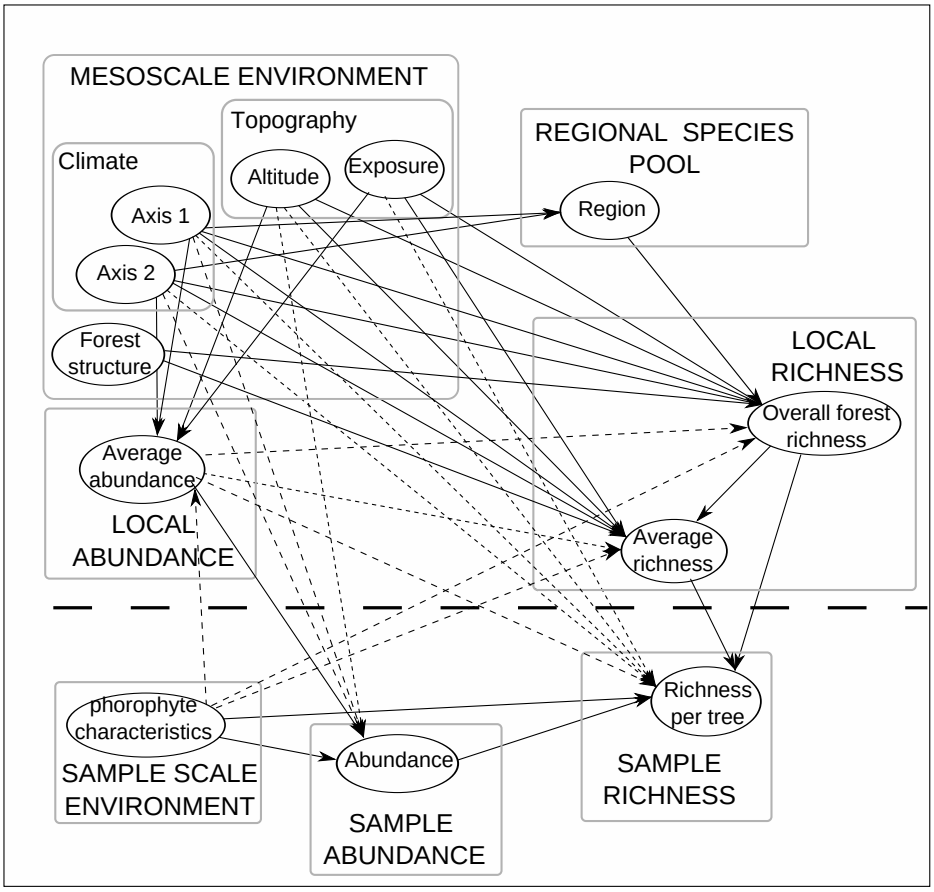

Figure 2.3: Scheme depicting the evaluated relationships. Variables in circles represent latent variables while rectangles represent categories and subcategories. Observed variables corresponding to the categories and latent variables are listed in Table 2.1. Arrows indicate hypothesized direction of causality. Dashed lines indicate paths expected to be non significant. Note that if no line is shown the relationship was not tested

and 100% cover. Species richness and abundance were correlated at both the local (spearman rho=0.15, p=0.09, for average forest richness) and sample (spearman rho=0.14, p<0.001, for richness per trunk) scales.

Effect of mesoscale climatic gradients over richness at the local scale

Climatic variables showed significant effects upon richness and abundance at the local scale. Explained variance reached 29% for overall forest richness and 22% for

Categories	Latent variables	Indicators
1 Biogeographic region	Region	Binary variable, either Mediterranean or Atlantic (see Fig. 2.1)
2 Mesoscaleenvironment		
2.1 Climate	Axis 1	Mainly related to SR, PIE, WT and AT (see supplementary material, Table A3)
	Axis 2	Mainly related to SR*PCRA and PCRA*WT (see supplementary material, Table A3)
2.2 Topography	Altitude	Altitude above the sea level in meters
	Exposure	Slope and aspect
2.3 Forest structure	Level of development	Development level according to the Spanish Forestry map
	Diameter	Average diameter, diameter variance
3 Sample scale environment	Phorophyte characteristics	Tree diameter at breast height and exposure in the tree at which the sample was taken
4 Diversity and abundance		
4.1 Local richness	Overall forest richness	Total number of species per forest
	Average forest richness	Mean richness per sample within each forest
4.2 Local abundance	Average abundance	Mean percentage of bryophyte cover per forest
4.3 Sample richness	Richness per tree	The number of species found in each sample
4.4 Sample abundance	Abundance per tree	Percent of bryophyte cover in each sample

Table 2.1: Variables included in the partial least squares path analysis by category. For details see methods and supplementary material

both average forest richness and average abundance (Table 2.2). In all, the richness and abundance regression models included six climatic variables related to water availability and temperature during winter and autumn: (i) mean spring rainfall (SR); (ii) pluviometric coefficient relative to August (PCRA; the higher the index the lower the severity of summer drought period); (iii) index of hydric continentality of Henze-Dieckmann (HCH; it has negative values in the area and increases with continentality); (iv) pluviometric index of Emberger (PIE; designed specifically for Mediterranean climates, the higher the index values the more Atlantic the climate is); (v) mean autumn temperature (AT) and (vi) mean winter temperature (WT). The residuals of the overall forest richness model showed no spatial auto-

Selected variables	Coef. sign	t	VIF
Overall forest richness (r^2 = 0.29***)			
Spring rainfall (SR)	-	$-2.74**$	2.83
Mean Winter temperature (WT)	+	-1.89	2.47
Pluviometric coefficient relative to August (PCRA)	+	1.70	1.18
SR * WT	+	$1.99*$	1.45
SR * PCRA	-	$-3.22**$	1.82
PCRA * WT	-	$-4.90***$	1.74
Average forest richness (r^2 = 0.22***)			
Pluviometric coefficient relative of August (PCRA)	+	$2.28*$	1.08
Pluviothermic index of Emberger (PIE)	-	-1.87	2.10
Hydric continentality index of Henze-Dieckman (HCH)	-	-1.18	4.67
Mean Winter temperature (WT)	-	-1.66	3.88
PCRA * WT	-	$-3.18**$	1.47
PIE * WT	+	$2.08*$	2.19
Average abundance (r^2 = 0.22***)			
Hydric continentality index of Henze-Dieckman (HCH)	-	$-2.56*$	1.15
Mean autumn temperature (AT)	+	$2.46*$	1.08
Pluviometric coefficient relative of August (PCRA)	+	$2.64**$	1.06

Table 2.2: Multiple regression models relating climatic variables to overall forest richness, average forest richness and average abundance. The table shows overall goodness-of-fit, sign of the coefficients, t values, and variance inflation factors (VIF). *** stands for p<0.001; ** for p <0.01; and * for p<0.05

correlation at any distance lag (not shown) evidencing that all spatially structured variation was accounted for by the variables selected in the models. In the average forest richness model there was a significant autocorrelation value at the 10^{th} lag (96.5 Km) and in the average abundance model, lags 1 (11.4 Km), 7 (69.9 Km) and 9 (86.0 Km) were significant. This could be indicating missing variables especially in the model for average abundance, although the complex topography of the studied area prevents from identifying them.

The regression models and the hierarchical partitioning analysis show that the relationship between richness and climate is very complex, as it includes a high number of interaction terms (Table 2.2). Also, the hierarchical partitioning result revealed some negative joint effects meaning that the combination of the two predictors forming the interaction with the dependent variable is synergic; that is, together they explain more than the sum of their separate effects. In general, water availability variables showed a major role in determining both richness and abundance. Variables related to temperature were also important especially for richness,

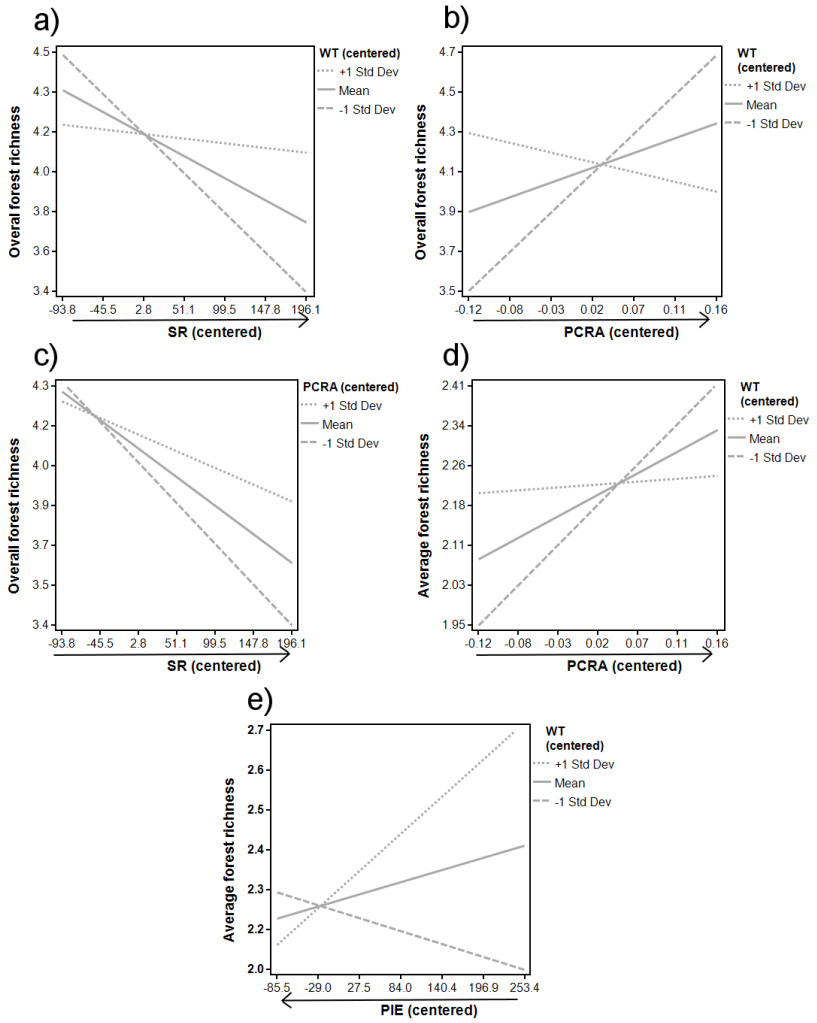

Figure 2.4: Interaction plots showing the effect of: (a) mean spring rainfall (SR) on overall forest richness at three levels of mean winter temperature (WT); (b) pluviometric coefficient relative to August (PCRA) on overall forest richness at three levels of WT; (c) SR on overall forest richness at three levels of PCRA (including WT as a covariate); (d) PCRA on average forest richness at three levels of WT; and (e) pluviometric index of Emberger (PIE) on average forest richness at three levels of WT. Variable codes as in the main text. Arrows below each graph indicate the direction towards conditions are more mesic

as they produce a change in the relationship between richness and water availability variables. The regression model for overall forest richness included three variables and three interaction terms (Table 2.2). Two of the marginal effects were related

to water availability (SR and PCRA); PCRA had a positive correlation with richness, but surprisingly SR was negatively associated with overall forest richness. The third marginal effect was related to energy input (WT) and showed a positive relationship with richness. As the slopes of the marginal effects in a model with interactions can be misleading it is important to analyze carefully the interaction terms to correctly interpret the effect of the marginal variables. The detailed analysis of the interaction between SR and WT (Fig. A1a) provided an insight into the complexity of the relationships between climate and richness; while at high WT SR had a positive effect upon overall forest richness, at progressively low WT the effect of SR was negative. That is, those forests with low temperatures and at the same time high water input during spring had, in general, low richness values. Finally, the interaction between PCRA and WT was also complex (Fig. 2.4b); at low WT the effect of PCRA was positive but when WT was high the effect of PCRA became negative. At low values of SR the slope of the relationship between PCRA and richness was steeper (Fig. 2.4c), meaning that the effect of summer drought severity was much more important in those localities with low rainfall during springtime. The results of the hierarchical partitioning analysis highlight the importance of these interaction terms (Fig. 2.5a). The only main effect with a strong independent effect was SR. Besides, the interactions of WT with PCRA and SR had large independent effects upon overall forest richness, even larger than the independent effect of PCRA and WT alone. The hierarchical partitioning analysis also showed that large proportions of the explained variation were due to joint effects, and relationships among variables in this model turned out to be very complex.

The model for average forest richness was composed of four main effects and two interaction terms (Table 2.2). Similarly to the overall forest richness model, three of the main effects were related to water availability (PCRA, PIE and HCH), while the other variable was related to energy input (WT). PCRA had a positive effect upon richness, while PIE and HCH both had negative effects. The two interaction terms in this model involved WT (Figs. 2.4d and 2.4e). At high WT values, PCRA had almost no effect on richness. Conversely, at low WT the effect was positive and with a steep slope (Fig. 2.4d). WT also changed the slope of the relationship of PIE with average forest richness (Fig. 2.4e). While at high WT PIE had a strong positive effect, at low WT an increase in PIE had a negative effect upon richness. This response is analogous to the one showed by overall forest richness as it implies that the localities with low winter temperatures and high precipitations

harbor poorer communities. In this case, the hierarchical partitioning analysis revealed that both interaction terms had the greatest independent contribution to the richness model, higher than any of the marginal effects alone (Fig. 2.5b). In this model the joint effects were relatively small.

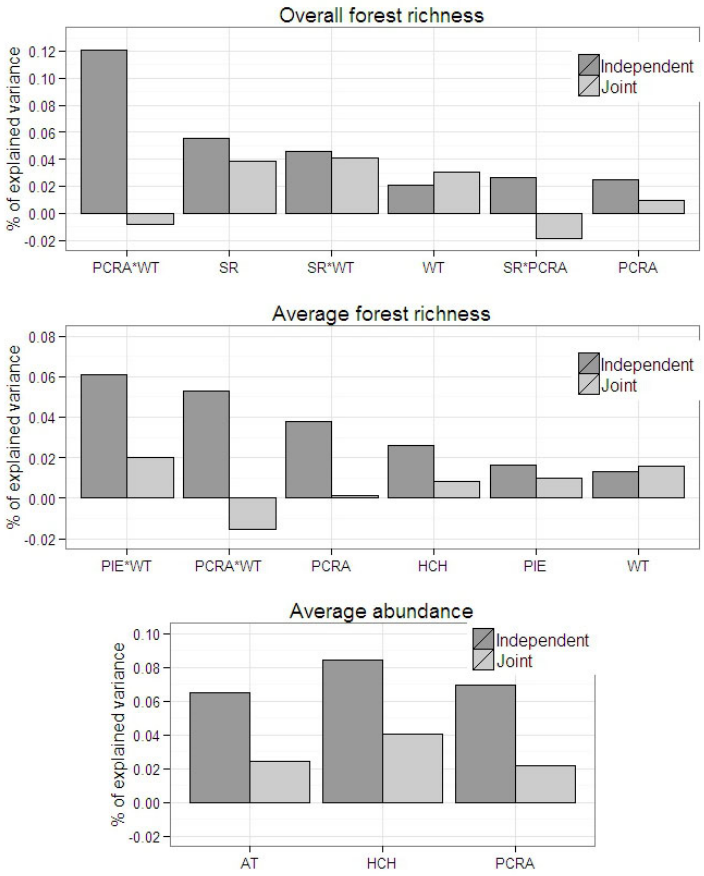

Figure 2.5: Independent and joint effects estimated by hierarchical partitioning of (a) overall forest richness (b) average forest richness and (c) abundance. Variable codes as in the main text

The regression model for abundance included three climatic variables but no interaction effects (Table 2.2). Two of the variables were related to water availability (HCH and PCRA) while the other one was related to energy input (AT). HCH negatively influenced bryophyte abundance, whereas both PCRA and AT had a positive effect upon richness (Table 2.2). Therefore, oceanic forests with attenuated summer drought and relatively high autumn temperatures have the highest bryophyte abundances. The hierarchical partitioning (Fig. 2.5c) analysis revealed

that the three variables had similar independent contributions upon average abundance, although the two variables related to water input showed a somewhat stronger effect on average abundance than the energy input variable.

The evaluation of the relative influence of all the factors on richness of epiphytic bryophytes at the local scale (Fig. 2.5, supplementary material) showed that climate and topography are the factors with the largest effect on bryophyte diversity at this scale. For overall forest richness the shared effect between climate and topography was the most important (13.3%), followed by the independent contributions of climate (5.5%) and topography (2.6%). Forest structure had a very small contribution (1.1%). Interestingly enough, although overall forest richness was significantly different between the Atlantic and Mediterranean regions (F=4.2, d.f.=109, p=0.04) the independent contribution of the biogeographic region after including the whole set of variables was close to zero. For average forest richness, topography was the factor with the highest independent contribution (12.3%), followed by its shared effect with climate (8.8%) and climate alone (3.4%). Forest structure had a very small independent contribution (0.8%). Although there were significant differences in average forest richness between Atlantic and Mediterranean regions (F=4.5, d.f.=109, p=0.03), region showed no independent effect on richness, but rather a small effect shared with climate (Fig. A4, Supplementary material).

Relationships among factors within and between scales

The PLSPA for richness and abundance measures at the local scale explained 20.5% of the observed variation in overall forest richness, 52.7% of average forest richness, and 16.3% of average abundance (Fig. 2.6). There was no effect of biogeographic region on any of the richness measures. Overall forest richness was influenced solely by climate and exposure. Average forest richness was related to climate, as well as to overall forest richness and average abundance. Average abundance was not influenced by climate but by topography and forest structure. Region showed no significant effect upon none of the richness measures when climate and regional effects were analyzed altogether (Fig. 2.6). For the parameters at the sample scale, the model explained 30.6% of richness per trunk and 38% of abundance per trunk. The abundance measure at the sample scale was related exclusively to average abundance while richness per trunk was related only to average forest richness. Overall, the strongest effects were the paths of overall forest richness over average forest richness and of this latter variable over richness per trunk, reflecting the importance of the hierarchical structure of richness measures across scales.

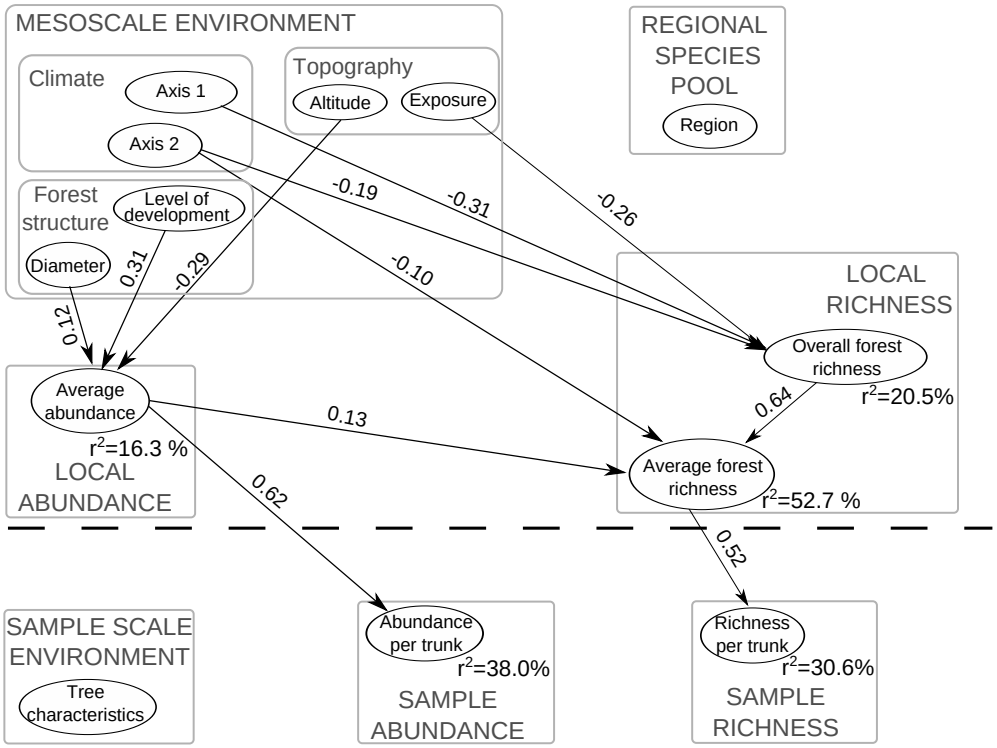

Figure 2.6: Partial least squares path analysis indicating all significant paths. Numbers above the lines indicate standardized path coefficients. The model initially evaluated is depicted in Fig. 2.3

2.4 Discussion

Effect of mesoscale climatic gradients over richness at the local scale

Our results evidence that climatic gradients and topography play a relevant role in shaping the richness of epiphytic bryophyte assemblages. However, our models explain *ca.* 30% of richness variation, a relatively low percentage that may be related to some missing variables. Determining which factors are responsible of the unexplained variability remains speculative at this point. However, we can draw some lines to deepen the knowledge about the geographical ecology of this group.

Given that we evaluated a large number of climatic factors and almost no spatial

autocorrelation remained in model residuals, it seems unlikely that any additional climatic variable has a relevant influence on richness. However, the inaccuracy in the climatic models can indeed be a source of unexplained variability. The complex topography of the territory creates an intricate mosaic of climates that cannot be described with precision at the scale of our analysis. Stand structure has been identified as a key factor for epiphytic bryophytes (Lara & Mazimpaka 1998, Mazimpaka *et al.* 2010). We don't expect this factor to have a major influence on the communities under study, as sampled forests were quite homogeneous (see Fig. A5). It seems most likely that the complexity of the studied landscape makes difficult to detect some of the environmental effects determining the coexistence of epiphytic bryophytes. Landscape properties such as forest fragmentation or connectivity (both past and present) are well-known to affect bryophyte diversity (Snäll *et al.* 2004, Pharo & Zartman 2007). Also, the dominant bryophyte species change drastically between the north-western part of the study area – where Atlantic conditions predominate – to the drier southeast – of Mediterranean influence (see below), a change in assemblage composition that could obscure the effect of humidity on richness that is commonly found in other areas. Last, but not least, the studied area has experienced pronounced human influence which may be obscuring the importance of the climatic effect.

Besides these uncertainties, the unpredictability of diversity patterns may in part be the result of dispersal and/or neutral processes causing stochastic fluctuations of bryophyte communities. Mota de Oliveira (2010) found that the diversity of epiphytic bryophyte communities in the Amazonian Basin was neither spatially structured nor correlated with environmental gradients, which led to the proposal that bryophyte assemblages may be structured by neutral processes. These results are quite divergent from those found in other regions (Wolf 1993, Vitt *et al.* 1995, Kessler 2000, Callaghan & Ashton 2008, our results). Although it seems clear that in our study epiphytic bryophytes respond better to climatic gradients than those in the Amazonian Basin, it is yet plausible that neutral dynamics are playing a relevant role also in our assemblages.

Previous analyses of the relationship between bryophyte richness and climate paid little attention to the selection of adequate climatic descriptors, relying mainly on annual variables (Vitt *et al.* 1995, Humphrey *et al.* 2002, Zechmeister *et al.* 2003, Callaghan & Ashton 2008 but see Aragón, Martínez & García 2012). This contrasts with the importance of considering seasonal climatic variability highlighted by Benzing (1998) or Asada, Warner & Pojar (2003), among others. Our

results confirm that seasonal climatic variability must be taken into account to gain a better understanding of the effect of climate on bryophyte diversity.

Water availability during the spring and summer drought severity were the most important climatic correlates of local richness in our study area. This agrees with numerous studies on bryophyte physiology (Proctor 2000, Proctor *et al.* 2007), species distributions (Ratcliffe 1968, Albertos 2001) and community composition (Gignac *et al.* 1991, Lara 1993, Albertos 2001). Winter temperatures are also important in determining bryophyte richness especially because they act as strong moderators of the effect of water availability. The localities with high rainfall during spring that also suffer low winter temperatures have relatively low richness, resulting in negative relationships between richness and water availability. The importance of low winter temperatures is perhaps surprising since bryophytes are able to grow in colder conditions than vascular plants (Furnes & Grime 1982, Rincon & Grime 1989). Even so, winter temperatures have been previously identified as having relevant effects on this group (Longton 1988, Gignac & Vitt 1990, Jonsgard & Birks 1993, Privitera & Puglisi 2008). Interestingly, the Atlantic part of the study area is characterized by species such as *Ulota crispa* and *Ulota bruchii* (Albertos 2001), which are typical of localities subject to oceanic influence and narrow thermic amplitudes (Dierssen 2001). The negative effect of winter temperatures may be related to the loose of oceanic species in the coldest localities of the study area. As a consequence these localities host impoverished assemblages in spite of having relatively high precipitations. These results are consistent with the hypothesis of a biotic relativity to water-energy dynamics, which states that since biological activity is supported by the availability of liquid water, and such availability is mediated by energy (in our case temperature), richness will be determined by the interaction of these two factors (O'Brien 1993, O'Brien 2006). Although the water-energy dynamics hypothesis was intended to explain large scale patterns, its effects may also be detectable at smaller scales (Whittaker *et al.* 2001), as shown by Moser *et al.* (2005) for vascular plants. Therefore it can be concluded that both water availability and temperature have a significant effect on bryophyte richness but it is the interplay between them which is most important.

The climate–richness relationship turned out to be complex in the study area. Here, we detected a change in the main limiting factor across the territory. While low temperatures constrain the capacity of sites with high precipitations to support more species by reducing the length of the growing season, the effect of summer drought was more severe in the localities that also have low rainfall during springtime. Thus, in the north-western region of the study area where temperatures are

colder the diversity of epiphytic bryophytes is limited by the energy input, whereas in the southeast the limiting factor turns out to be water input. Such a change in the main limiting factor also determines the composition and structure of bryophyte assemblages, which vary from the drought-tolerant Mediterranean species with compact growth forms of the genus *Orthotrichum* that are predominant in the south-east, to the mesic Atlantic species of pleurocarpous mosses and liverworts that are more common in the north-west (Albertos 2001, Albertos *et al.* 2005).

Relationships among factors within and between scales

Our results show that the effects of climate, topography and forest structure account for richness and abundance variations at the forest scale.

We did not find a strong relationship between richness and abundance and contrary to our previous expectation the effect of abundance on species richness occurs at the forest rather than at sample scale. Positive correlations between both community descriptors have been previously reported (Bergamini *et al.* 2001, Patiño *et al.* 2009) but no clear relationship between bryophyte richness and abundance can be deduced from the literature as unimodal relationships have also been described (Ingerpuu *et al.* 2003, Löbel *et al.* 2006). Due to the nature of our data we cannot assess whether the communities under study are driven by facilitation or competition nor if there is lack of strong interactions between species. However, regardless the nature of any interaction, as the relationship between richness and abundance is weak and positive it seems that the biotic interactions are not sufficient to limit species richness.

The different factors influencing bryophyte communities display a strong hierarchical structure in our study area (see Fig. 2.6). Remarkably, factors at the mesoscale (climate, topography and forest structure) have indirect effects on richness and abundance at the within-forest (sample) scale, through their direct effect on richness and abundance at the local scale. The importance of large-scale processes on the diversity and dynamics of local communities is well-known (Ricklefs 1987, Ricklefs 2004, Ricklefs 2007), in particular the importance of the regional propagule supply for maintaining local richness is widely recognized (e.g. Mouquet & Loreau 2003, Hortal *et al.* 2009). However, as Harrison & Cornell (2008) point out, these top-down relationships should not only be evaluated at very large spatial extents but also within regional to local scales, as these are the scales at which mesoscale influences and ecological processes meet each other. Our results show

that richness at small scales is indirectly related to mesoscale climatic gradients, through the effect of these mesoscale factors on local richness.

Such hierarchical variations in the importance of the different factors influencing diversity are in accordance with other works using similar multi-scale theoretical frameworks (Cornell 1993, Harrison & Grace 2007).

The lack of importance of small scale factors in our analyses should be taken with caution. Our work was focused mainly on detecting the scaling down of mesoscale effects and therefore small scale environment was measured less accurately than mesoscale enviroment. A possible indicator of the potential importance of microclimatic conditions on bryophyte diversity comes from the effect of forest structure on abundance and richness. In the ordinal classification we used, changes in forest structure imply an evolution of the forest to more humid and shady conditions. These microclimatic differences may be enough to constrain the growth of some mesic species (such as the liverwort *Metzgeria furcata* and the mosses *Ulota bruchi*, *U. crispa*, *Orthotrichum pumilum* and *O. rupestre*), and limit their abundance, but not to exclude them from trunk assemblages, so bryophyte richness will not vary significantly between forests with different levels of development. Further work should be directed to improve the characterization of the tree scale environment including tree-specific measures of light availability, temperature and humidity. Finally, an accurate characterization of environment at various scales would allow going a step further and evaluating joint interactions at various scales

It is important to note that the model we propose is based on some strong assumptions, such as the directionality of the hierarchical relationships across scales. Our results indicate a lack of saturation of the communities at the small scales. On the one hand, the relationship between richness and abundance is weak. On the other, the relationship between local and regional richness is linear even at the higher levels of richness – where strong interactions between species are more likely – (see Fig. A6) which can be an indication of unsaturated communities (Harrison & Cornell 2008). Further, strong limitations from small to larger scales could appear if there were strong relationships between local factors (biotic or abiotic) and richness; we have found no evidence of such relationships, although we must note that there is room for improvement in the description of the small scale environment. Despite such uncertainty, all these evidences point to a little influence of small-scale interactions on richness at the larger scales, thereby indicating a top-down hierarchical relationship between diversity at different scales. Besides the abovementioned limitations, this type of analysis can prove useful to study how different effects are related through different spatial scales (Harrison & Cornell

2008, Kissling, Field & Böhning-Gaese 2008, Spitale, Petraglia & Tomaseli 2009, Gazol *et al.* 2012).

2.5 Concluding remarks

In summary, our results evidence that climate plays a relevant role in shaping epiphytic bryophyte richness as it has a strong direct effect upon richness at the local scale. Here, seasonal variation of climate plays a major role on shaping bryophyte diversity gradients. It is the interplay between water availability and energy (precipitations and temperature in our analysis) what regulates richness in the area given that none of the individual climatic variables showed a strong independent effect upon richness. These effects of climate and topography scale down from local richness to sample richness: climate and topography constraint local richness, and since local richness limits sample richness the effect of climate and topography is transmitted from the local to the sample scale.

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CHAPTER

3

Designing bryophyte surveys for an optimal coverage of diversity gradients

Abstract Knowledge on the distribution and abundance of species is plagued by significant taxonomic and geographic biases that influence the analyses on biodiversity patterns. Due to this, standard, easy-to-use methods are needed to design efficient field campaigns that minimize data deficiencies. We evaluate the applicability, usefulness and effectiveness of a survey design protocol based on the Environmental Diversity criterion (ED) under different scenarios, with examples of varying extent of environmental niche, range of spatial distribution and level of previous knowledge. We planned surveys for epiphytic bryophytes growing in three types of forests at NW Iberian Peninsula (dominated by *Quercus ilex*, *Q. faginea* and *Q. pyrenaica*). Knowledge on the distribution and abundance of epiphytic bryophytes in this region presents large gaps and strong geographic biases. Besides, the three forest types differ in their environmental requirements, spatial distribution and level of previous knowledge, providing three working scenarios to test the response of the protocol under different situations. The protocol was implemented as a set of sequential selection rules, starting by an ED-based criterion aiming at maximizing the coverage of climatic and geographic variability; further criteria include an iterative set of qualitative properties: maximizing forest area, conservation status and accessibility. The protocol performed efficiently at different ranges of spatial distribution levels of environmental variability, and degree of previous knowledge and generated an even distribution of sampling points that efficiently covered the diversity of epiphytic bryophytes. The results show that ED protocols are a proficient and time-saving approach to select sampling sites by objective criteria also for groups with high dispersal ability and fragmented landscapes.

3.1 Introduction

Current knowledge on species numbers, their distribution and abundance is scarce (i.e., the Wallacean Shortfall; Lomolino 2004). Despite the great effort made over the last decades on data gathering, knowledge on species distributions is far from being complete (Rocchini *et al.* 2011). In general, lack of knowledge is greater as the organisms decrease in size and complexity (Whittaker *et al.* 2005; Fontaneto & Hortal 2013), declining from vertebrates to invertebrates (Medellín & Soberón 1999; Ødegaard 2000; Lambshead & Boucher 2003;) or from vascular plants to bryophytes (Mutke & Barthlott 2005; von Konrat *et al.* 2010). But the bias is not just taxonomic; many areas remain under-surveyed at worldwide, regional and local scales. Even the groups of species that accumulate the highest amount of information, such as birds or mammals, have large information gaps (Reddy & Dávalos 2003; Whittaker *et al.* 2005; Schulman, Toivonene & Ruokolainen 2007). All these biases and limitations together cause misrepresentations of the distribution and responses to the environment of most species (Hortal *et al.* 2008; Rocchini *et al.* 2011; Ladle & Hortal 2013), and are likely to produce spurious results when data are used for modeling and pattern analysis (see e.g. Soberón and Peterson 2004; Hortal, Lobo & Jiménez-Valverde 2007; Mutke & Geffert 2010; Leitão, Moreira & Osborne 2011).

A direct consequence of the limitations of biodiversity data is the need for advancing in the development of survey design protocols explicitly directed to increase the evenness and quality of these data. In order to improve the available information, researchers face the question of how to select sampling sites for an adequate representation of biodiversity (Funk, Richardson & Ferrier 2005; Hortal & Lobo 2005), a task hindered by the inherent complexity of the biodiversity patterns and the unbalanced nature of the data at hand. Here, two main strategies have been used to design field campaigns, directed to either obtaining complete local inventories or maximizing the spatial coverage of species (and ecological) turnover: i) to analyze the completeness of the local inventories and focus the survey on areas with incomplete inventories (Reddy & Dávalos 2003) or ii) to use environmental variables as proxies of biodiversity in the expectation that covering the environmental variation within the region will maximize the proportion of biodiversity in the study area that is effectively sampled (Austin & Heyligers 1989; Ferrier & Watson 1997).

For bryophytes the approach of inventory completeness has been successfully applied in cases with high background knowledge (Hill & Dominguez Lozano

1994; Callaghan & Ashton 2008). However, this type of approach has some important limitations. As the analysis is based on known species distributions, if the records are biased, the results may be inaccurate or even flawed. Besides, the completeness approach identifies the poorly surveyed areas but does not help to prioritize among unsurveyed sites. Recently there have been attempts to combine the analysis of inventory completeness and the use of environmental variables as proxies of species diversity. Briefly, Aranda & coworkers (2011) first identify the well surveyed and the undersurveyed localities; then they stratify the environmental space using a partitioning technique; finally, they cross the information at these two levels and select the sampling sites that complete the gaps in the environmental and geographic space. As the authors note (Aranda *et al.* 2011), using a classification to stratify the environmental space has some disadvantages: i) it is based on a partial representation of the environmental space instead of the whole set of conditions, ii) it is strongly dependent on the clustering algorithm and the number of final divisions (see also Hortal & Lobo 2005).

We present an Environmental Diversity (ED)-based protocol, developed from the general proposal of Hortal & Lobo (2005) that combines the analysis of degree of completeness and the use of environmental variables without undertaking a previous classification of the environment. This protocol takes full advantage of information on the previously recorded localities to determine which areas of the environment and spatial spectra best complement the well known localities. To test this protocol we used a group of organisms with high dispersal ability and large survey gaps: the epiphytic bryophytes growing in tree trunks of oak forests at the Spanish Tagus and Duero basins (Fig. 3.1). Oak forests within the study area consist mainly of three heterogeneous forest types (i.e. forests dominated by *Quercus ilex* L., *Q. faginea* Lam. and *Q. pyrenaica* Wild.). These three forest types differ in their environmental requirements, spatial distribution and level of previous knowledge.

Therefore, they provide three different working scenarios to evaluate the response of the protocol. The specific aims of this work are therefore: a) to evaluate the applicability of the ED protocol proposed by Hortal & Lobo (2005) for organisms with high dispersal ability such as bryophytes in a strongly fragmented landscape, b) to test the performance of the ED protocol proposed by Hortal & Lobo (2005) at different levels of environmental variability, ranges of spatial distribution and levels of previous knowledge; and c) to locate a set of comprehensive, adequate and representative sampling sites to improve the knowledge on epiphytic bryophytes of the Iberian Peninsula.

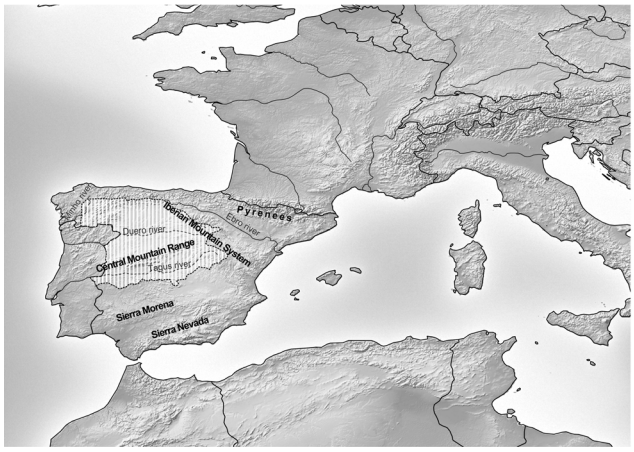

Figure 3.1: The Iberian Peninsula showing the most important rivers and mountain ranges. The study area is indicated in light grey

3.2 Methods: Protocol description

The protocol is divided in three parts (main steps are summarized in Fig. 3.1. The first part (step 1.1 to step 1.4) is devoted to the compilation of available biotic and abiotic information and the selection of the best surrogates of biodiversity. The second part (step 2.1 and step 2.3) consists in the actual selection of the territorial units to be surveyed, which is done through an iterative multicriteria protocol. Finally, the third part is devoted to the evaluation of the results (Part 3).

Part 1.- Compilation of available information

Step 1.1- Grain and extent of the study area

Both biodiversity patterns and the processes affecting them may change with the scale of analysis (Pausas & Austin 2001; Whittaker, Willis & Field 2001; Willis & Whittaker 2002; Rahbek 2005; Hortal *et al.* 2010). As a consequence, when designing field campaigns it is crucial to adjust the extent, grain and intensity of the survey to the objectives and the organisms under study.

The extent is the size of the study area, and defines the amplitude of the environmental and geographic gradients that need to be covered by the survey. It thus depends on the objectives of the study and the type of gradient under analysis, so that the larger the gradient the larger the extent needed to cover it. Once the extent is defined it is necessary to choose the grain (sensu Whittaker *et al.* 2001), or in other words, the territorial units or sampling sites at which data will be collected.

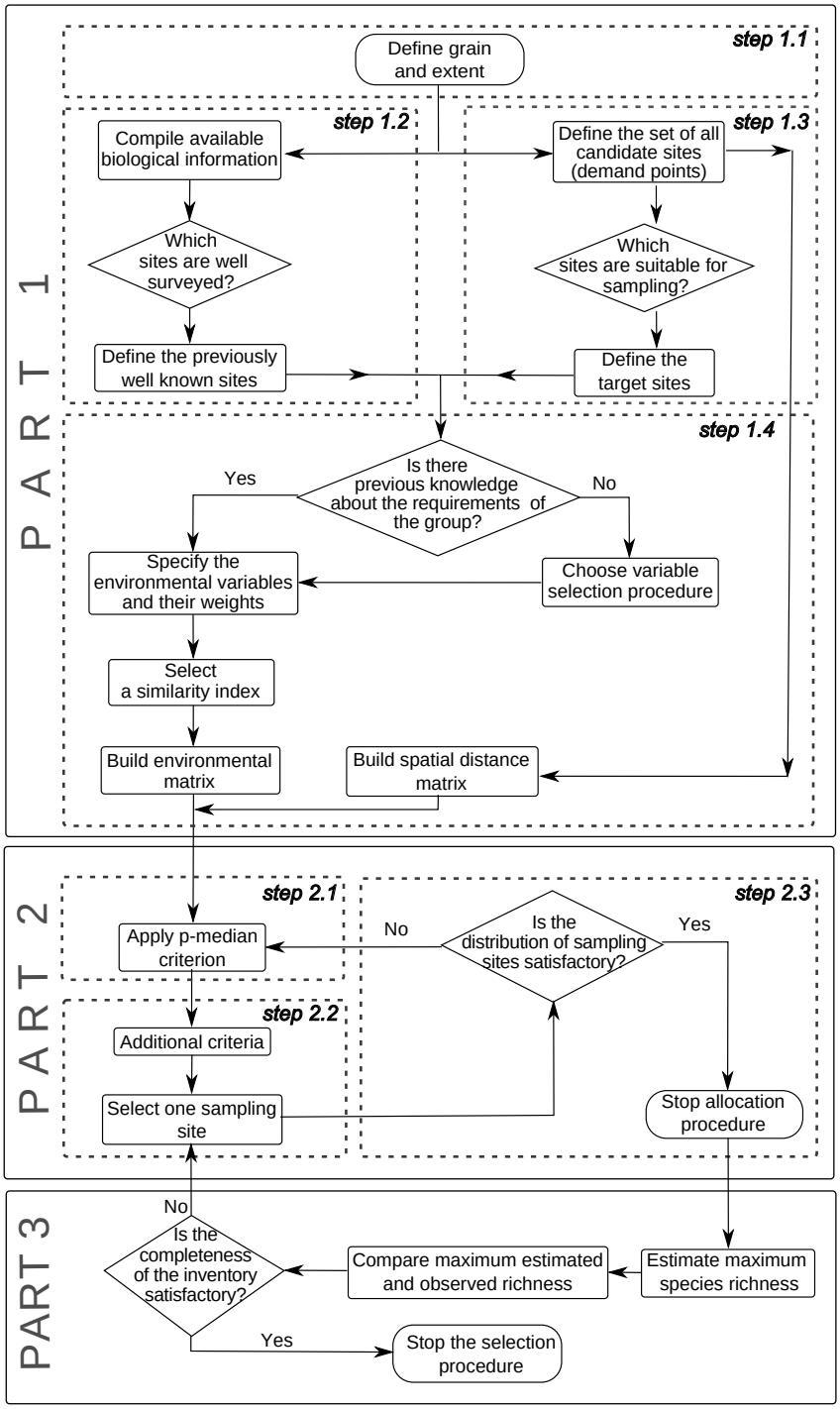

Figure 3.2: Scheme of the survey design protocol. Dashed quadrats indicate steps within the protocol.

Territorial units need to be meaningful for the organisms and the processes under survey. If they are too large the patterns of biodiversity variation may be obscured or blurred by the within-unit internal variability, making the surveys designed that way useless. If, on the contrary, territorial units are too small, the observed pattern may be affected by the noise caused by processes acting at a scale different to the environmental data.

Besides the size, form and nature of the territorial units are also critical. Quite often the basic units are regularly distributed quadrats in a geographical grid with homogeneous size (Hortal & Lobo 2005). However, in the case of organisms growing in discontinuous and well defined units, discrete landscape or vegetation patches may also be used. To illustrate the application of the protocol we designed the survey for the study of epiphytic bryophytes in the NW quadrant of the Iberian Peninsula. The aim of these surveys was to analyze which factors (climate, landscape connectivity, forest structure, tree characteristics etc.) influence the variations in the biodiversity of epiphytic bryophytes along a Mediterranean gradient. Due to this, the extent of the area was delineated to comprise the limit with the Atlantic region in the NW and the central part of the Mediterranean climate of the Spanish territory. Therefore, we included the Duero and Tagus basins plus a small area of the Minho basin in the northwest of Spain (Fig. 3.1). With ca. 150,000 km^2, the study area covers more than $\frac{1}{4}$ of the Iberian territory and comprises an important climatic gradient, from the central part of the Iberian Peninsula with a typically Mediterranean climate up to the limit with the Atlantic climate in the north. Regarding the grain, we selected forest patches as territorial units because in the study area (a highly fragmented landscape) they represent discrete entities within a matrix of unsuitable landscape for epiphytic bryophytes.

Step 1.2.-Selection of the previously surveyed areas

The first step after defining the scale of analysis is gathering the available information on the area and the taxon under study. This is critical when applying the ED protocol, as the algorithm used to select the sampling localities (see step 2.1) evaluates the gain in the represented geographic and environmental diversity when adding a new locality to an existing pool of well surveyed localities (initial sites from now on) (Faith & Walker 1996; Faith Ferrier & Walker 2004). Usually, information on species distribution is heterogeneous and scattered among various sources. As a consequence, gathering data on the presence and abundance of species for a region entails an intensive search and requires building complex databases. When data comes from heterogeneous sources, species accumulation curves

have been successfully used to identify well sampled localities, that is, those localities that accumulate enough records proportional to the existing species diversity (see for example, Hortal & Lobo 2005). But some important limitations exist since many databases lack accurate information on the sampling effort (see e.g. Hortal *et al.* 2007). Even more, some databases may lack observational data or duplicate site records. In these cases, other methods such as expert knowledge may apply, since building accumulation curves is unfeasible.

As the final intention of our surveys is to study the effect of climate and forest structure on bryophyte diversity, we constrained the search of formerly-surveyed sites to those coming from works with field sampling methods comparable to the ones to be used in the new survey (see e.g. Lara 1993 & Albertos *et al.* 2005 for more information on field sampling methods). We selected the most relevant localities of the studies done during the last 20 years that included sampling sites within our study area. The final selection consisted of data from 3 PhD and a MSc thesis project (Lara 1993; Albertos 2001; Albertos *et al.* 2005; Cortés 2005; Medina *et al.* 2013) and comprised 42 forests (i.e. initial sites see below) and ca. 5500 records (here, there is a record for each species in a sample and there are around 20 samples in each forest).

Step 1.3.- Defining demand and target sites

The complete set of territorial units available for survey (demand sites from now on) defines the sampling area and the environmental and geographical space to be analyzed. For example, all the UTM quadrats within a study area and the temperature and rainfall values of those quadrats. However, it is frequently the case that some sites are unsuitable for sampling because of limitations unrelated to the objectives of the study. For example, in a sampling design in the Guyana, Funk & coworkers (2005) had to discard some sites due to political reasons. As they removed those sites in the initial steps of the analysis the final selection was done without including the full environmental and spatial spectrum of interest. The approach presented here allows a more inclusive alternative that avoids discarding those points since, following Hortal & Lobo (2005), it includes as demand sites the whole territory except only the well sampled areas. Before running the analysis the user defines a subsample of sites as suitable for sampling (target sites from now on) from the whole set of available territorial units or demand sites. The ED protocol will set up the environmental and spatial extent of the analysis to all demand sites, so that the full gradient within the study area will be considered. However,

only territorial units included within the set defined as suitable (target sites) will be selected.

We defined the set of demand sites for epiphytic bryophytes growing on tree trunks in oak forests in our study area according to the data in the digitized version of the Spanish forestry map (Ruíz de la Torre 2001), a GIS layer that contains information on all the wooded areas of Spain. We first removed all forest patches dominated by species out of the scope of this study (mainly pine groves). After removing them, there were more than 10,000 forest polygons potentially adequate for our surveys within the study area (Fig. 3.1). Here note that, because the design of the Spanish forestry map was based on 1:50,000 topographic maps, polygons in different map sheets with the same characteristics are stored as separate entities. Also, the forestry map records more than 15 fields on the ecology and structure of the forests. Due to this, we merged all adjacent polygons with the same dominant species, conservation status and similar canopy cover, in order to simplify such information and adapt it to the purposes of our study. The resulting GIS layer included 6669 *Quercus*-dominated forest patches potentially adequate for our surveys (demand sites) that define the environmental and geographical space to be represented (see Fig. 3.3). This implies that we assume that these forest patches represent the potential distribution of habitats suitable for epiphytic bryophytes growing in oak trees in the study area, therefore constituting the environmental and geographical space that we aim to cover with our surveys.

As in the case of Funk & coworkers (2005) some sites were not adequate for sampling in our study area. The most important constraint was related to human transformation of the landscape. Some of the forest patches depicted in the forestry map were very small, while others had a poor conservation status and were either very open forests or consisted of small-sized trees where communities of epiphytic bryophytes do not develop well (Barkman 1958; Lara & Mazimpaka 1998; Garcia, Sérgio & Sim-Sim 2005; Mazimpaka *et al.* 2010). Consequently, we defined the target sites as those forests that presented a set of characteristics that favor the development of epiphytic communities, that is, forests with more than 1 km^2 of extent and high values of conservation status, equal to or higher than 5 (the scale goes from 0 for no vegetation cover at all to 9 for forests with complex structure but note that, in practice, levels above 7 are very exceptional), and with trees of more than 3 meters in height.

Step 1.4.- Environmental and geographical data

Once the demand, target and previously surveyed (herein initial) sites are established, it is necessary to build the matrices with the environmental and geographic information. A critical step when building an environmental matrix is the selection of the variables used to define the environmental space. The selection should be specific to the organisms and the scale of analysis. Here, using a few variables with known impact on the target organisms and weighting them regarding their importance is recommended (Hortal & Lobo 2005). Once the most adequate variables have been selected, a metric to account for the environmental similarity (or dissimilarity) among sites has to be chosen. Although Euclidean Distance has been typically used for this task, other measures such as Gower similarity coefficient (Legendre & Legendre 1998) may be preferable, as they allow including qualitative variables and giving them weights to account for their relative importance (Hortal & Lobo 2005).

Apart from environmental factors, the selection of sites to survey must to take into account geographic variability. Spatially distant but environmentally similar sites may hold very different species assemblages due to historical contingencies and biotic dynamics. Hence, geographic variations should be included in the selection of survey sites, either as simple Euclidean distances (Funk *et al.* 2005; Hortal & Lobo 2005) or as more complex connectivity measures that take into account the geographical barriers (mountains, river basins etc.) that separate the target sites.

To select the most important abiotic factors affecting the biodiversity of epiphytic bryophyte communities we took into account former work analyzing environment-biodiversity relationships in this group within the study area and adjacent locations (Lara 1993; Albertos *et al.* 2005; Draper *et al.* 2005, 2006; Medina *et al.* 2013), as well as our expert knowledge on the relative importance of each variable. First we calculated the centroid of the polygons of all forest patches, to then extract the values of the climatic variables compiled by Hijmans & coworkers (2005) for each centroid. Here note that the resolution of Hijmans' maps –*ca.* 1 km^2– is in the order of magnitude of the size of most forest fragments –typically between 1 and 3 km^2 (Table 3.1). Then, we grouped these variables on classes representing precipitation, temperature and productivity (Table 3.1). We used the Gower similarity coefficient (Legendre & Legendre 1998) to calculate environmental distances between pairs of demand sites.

To give a specific weight to the selected variables we first defined three variable groups (Table 3.1), namely variables related to: (a) water availability (BIO12, BIO15, BIO17); (b) energy input (BIO1, BIO5, BIO8); and (c) productivity (NDVI).

	Q. ilex (n=2,959)	*Q. faginea* (n=785)	*Q. pyrenaica* (n=2,925)
Annual Mean Temperature (°C) BIO1	12.7±1.9	11.0±1.0	10.8±1.6
Max Temperature of Warmest Month (°C) BIO5	29.9±2.4	27.8±1.6	26.0±2.2
Mean Temperature of Wettest Quarter (°C) BIO8	9.4±2.3	10.0±2.1	6.9±2.4
Annual Precipitation (mm) BIO12	486.6±98	503±71	795±243
Precipitation Seasonality BIO15	35±7	27±4	35±8
Precipitation of Driest Quarter (mm) BIO17	59±21	80±20	100±29
Normalized Difference Vegetation Index (NDVI)	191±8	192±7	204±7

Table 3.1: Variables used to characterize the environmental space of the study area and their range of variation in the three forest types. Numbers indicate average ± standard deviation for environmental variables and lower quartile, median and upper quartile for size of the forest patches

Then we gave equal weight to each category; that is, $1/9$ weight to each one of the six variables in the water availability and energy categories and a weight of $1/3$ to the only variable in the productivity category. To account for the effect of the historical and other contingent factors we built a pair-wise Euclidean geographic distance matrix. Finally, we standardized the environmental and geographic matrices and multiplied them, to obtain a distance matrix that accounted for environmental and spatial variations altogether (M distance matrix in step 2.1).

Part 2.- Iterative selection procedure

The next steps describe the iterative part of the protocol (see Fig. 3.2). The procedure is as follows: each criterion (*p*-median and other built-in criteria) will be applied sequentially in a hierarchical way, so that one site from the set of *m* available sites is finally selected in each loop; then, the criteria will be applied again with *m*-1 sites. In the final step an adequacy measure is included to evaluate if the selected forests capture a sufficient proportion of the environmental variability.

Step 2.1.- *p*-median of spatial-environmental matrix

The first criterion to be applied within the iterative part of the procedure is the *p*-median selection algorithm (see Church & Sorensen 1996; Church 2002; Cova & Goodchild 2002). The *p*-median algorithm selects p localities from a set of *t* target sites in order to maximize the complementarity between the previously known

sites and the selected ones, in terms of environmental and geographic characteristics (note that more than one site is selected in this step). Therefore, the algorithm selects those localities that maximize the reduction in the total amount of variability of the forests that will remain unsampled after the selection (demand sites). Here, variability among sites is described by a matrix of distances M (either geographical or environmental, or both into a unique matrix). When the distance matrix M describes environmental differences, this algorithm effectively produces an environmentally stratified sampling design, as the *p*-median criterion will describe the localities regarding their environmental variability, selecting the samples so that they represent as much of the whole variation of the environmental diversity as possible, alike the strata in a classical stratified design.

The selection of the type of algorithm used to solve the *p*-median problem has been a controversial issue (Faith & Walker 1996; Araújo, Densham & Humphries 2003; Faith *et al.* 2004; Hortal & Lobo 2005; Hortal, Araújo & Lobo 2009). If the environmental gradients present in the study area are similar to or larger than the breadth of the species' fundamental niches, a continuous algorithm that assumes unimodal responses of species may be preferred. On the contrary, if species are expected to show discontinuous responses to environmental gradients or the full breadth of their environmental responses are not covered (Hortal *et al.* 2009) then a discontinuous algorithm may be preferable.

Further, the *p*-median algorithms can be either interchangeable or greedy; while the former produces a unique solution in one step, the latter selects one (or a few) target sites at each of a series of iterative steps. Although interchangeable algorithms are more likely to be closer to a global optimum, the number of sites to be selected should be defined a priori; otherwise the user has to perform several runs with different numbers of selected sites. In contrast, greedy algorithms are less time and resource consuming and have some practical advantages over interchangeable ones: i) since sites are selected one by one it is possible to evaluate the amount of variability covered by each one of them, and ii) the number of finally selected points can be set a posteriori. This can be done during the selection process, but, since these algorithms provide a hierarchy in the importance of each selected site, the implementation of the demanded features can be stopped according to an external criterion.

Here we adopt a pragmatic approach, assuming that this choice should be made in relation to the purpose of the analysis. For our study we selected a greedy, discontinuous algorithm. The discontinuous formulation was preferred because the

nature of the forest patches in the Iberian Peninsula is markedly discontinuous. Besides, a number of bryophyte species have their distribution limits in the Mediterranean area, so it is unlikely that the distributions of species and their responses to the environmental gradient have unimodal and continuous patterns. Our choice of a greedy algorithm lies in the practical advantage that gives the hierarchical selection of sites. If the selected sites are surveyed following such hierarchy –or the resulting samples are identified following it–, the survey and/or the taxonomic work can be stopped during fieldwork due to time or manpower constraints, avoiding significant biases in the coverage of the environmental or geographical variability finally obtained with the samples (see also Hortal & Lobo 2005). Nonetheless, this kind of algorithms can be easily implemented as one of a set of additional built-in criteria within an iterative selection criterion (see below).

Step 2.2.- Additional criteria

After applying the *p*-median criterion, a series of additional rules can be implemented to choose the most adequate site among the ones selected in the previous step. These rules can be either quantitative or qualitative and will be defined according to the purposes of the study (see recommendations on the type of rules in Hortal & Lobo 2005). If the sites are equivalent in their characteristics regarding the additional criteria the site in that step will be selected at random (note that one site is selected in this step).

The additional criteria for the study we present were based on four forest patch characteristics that were applied hierarchically: (1) maximization of conservation status, (2) area (3) circularity and (4) minimization of distance to roads. These variables, area and circularity were extracted from the polygons of the GIS layer of the forestry map (Ruíz de la Torre 2001). Distance to roads was calculated as the minimum distance from the roads to the centroids of the forest patches, calculated with a GIS layer depicting the main roads obtained from a digital topographic map of the Spanish Instituto Geográfico Nacional (IGN 2009). The first criterion aims to maximize the conservation status of the selected forests, while the second and third criteria were used in order to minimize the border effect. Finally, if two or more forests were equivalent in the rest of the characteristics, we chose the most accessible forest (minimum distance to road) to minimize survey costs. +

3.2.0.2 **Step 2.3- Stopping rule**

A critical step in the procedure is the selection of a threshold criterion (or stopping rule) at which a reasonable level of spatio environmental representation of the study area is achieved. Different cut-off levels can be defined on the basis of amount of spatio-environmental distance that is left uncovered each time a site is included (see Hortal & Lobo 2005; Medina & García 2010). The researcher should adjust the cut-off levels to the different objectives and available time and economic resources. In our study case we evaluated the protocol at the predefined threshold levels of cut-off10 (10% of uncovered variability) and cut-off5 (5% of uncovered variability).

Part 3.- Evaluation of survey success

The effectiveness of the protocol can be evaluated by analyzing completeness of the inventories at each cut-off level in the step 2.3. This can be done by comparing the maximum number of expected species to the observed species. There are several methods to estimate the maximum number of species on the basis of a presence-absence matrix (see e.g. Gotelli & Colwell 2001; Longino, Coddington & Colwell 2002; Díaz-Francés & Soberón 2005). In the one hand, methods based on species accumulation curves relate the cumulative number of species and the sampling effort by means of an asymptotic function, assuming that the extrapolated asymptote is a good estimate of the maximum species richness. In the other, methods based on non-parametric estimators rely on the rate of rare and infrequent species to estimate the probability of finding additional species. Non-parametric methods seems to be more widely accepted, as yet, there is no consensus around a single estimator and the decision should depend on the grain size and the type of available data (Hortal, Borges & Gaspar 2006).

The next step would be to compare the maximum estimated richness with the observed richness at each cut-off level and calculate the sampling effort needed to reach the required level of completeness (Chao *et al.* 2009). The researcher has to establish what is acceptable for the purposes of the study. Cardoso (2009) suggested three levels of completeness regarding the percentage of observed species over the maximum richness. Other authors preferred using 80% of completeness as threshold level (Aranda *et al.* 2011). Here, no gold standards can be applied as the decision should be in accordance with the objectives and the available resources.

For the study of epiphytic bryophytes, first we collected and identified samples until 10% of the spatio-environmental matrix of each forest type remained unrecovered (cut-off10). Then, we estimated the expected maximum species richness

for each forest type with Chao2 estimator (Hortal *et al.* 2006). Finally, we applied the procedure in Chao & coworkers (2009) to estimate what will be the completeness at the next cut-off level (cut-off5).

3.3 Results

The selection started with 6669 forest patches; 2243 of them fulfilling the minimum conditions to be sampled (good conservation status and a minimum area, see protocol description step 2.2 and Table 3.2). Overall, there were 42 initial sites. We made separate selections for the forests dominated by each *Quercus* species. In total, the procedure selected 26 additional forest patches to recover 90% of the overall environmental and geographical variability (cut-off10) and 76 forest patches to recover 95% of the variability (cut-off5) (Table 3.2). The number of selected points and their distribution were very different among the three forest types.

Forest type	Demand sites	Target sites	Initial sites	Selected sites	
				Cut-off10	Cut-off5
Q. pyrenaica	2959	1011	20	3	13
Q. faginea	785	373	2	9	17
Q. ilex	2925	859	20	14	45
Total	6669	2243	42	26	76

Table 3.2: Number of forest patches in each category of the selection procedure.Cut-off10: Number of selected sites when the uncovered variability of the environmental distance matrix equals 0.1. Cut-off5: Number of selected sites when the variability of the environmental distance matrix equals 0.05

Quercus pyrenaica forests showed a relatively high number of demand sites (Table 3.2). Consequently, the environmental and geographical variability within the study area was relatively high (Fig. 3.3a, Table 3.1). The number of initials was high (Table 3.2) but they were unevenly distributed throughout the region; 17 points were located in the centre of the study area (Central Mountain Range, see Figs. 3.1 and 3.3a) and 5 in the NW (see Figs. 3.1 and 3.3a). The decay in the distance matrix started with a relatively low uncovered variability (16%) due to the high number of initial forests (Fig. 3.4a). Then, the selection protocol produced a strong decay in the uncovered variability in the first selected forests (Fig.3.4a), followed by a gradual diminution in the rate of decay. The cut-off10 level was achieved with 3 additional forests, which left uncovered 22% of the environmental variability and

35% of the spatial variability (Fig. 3.4a). At this level the completeness of the inventory reached 89% of the maximum species richness (Table 3.3). The cut-off5 level was achieved with 13 additional forests (Table 3.2, Fig. 3.3a). At this level 12% and 27% of the geographic and environmental distances remained uncovered (Fig. 3.4a) and 95% of inventory completeness is expected (Table 3.3).

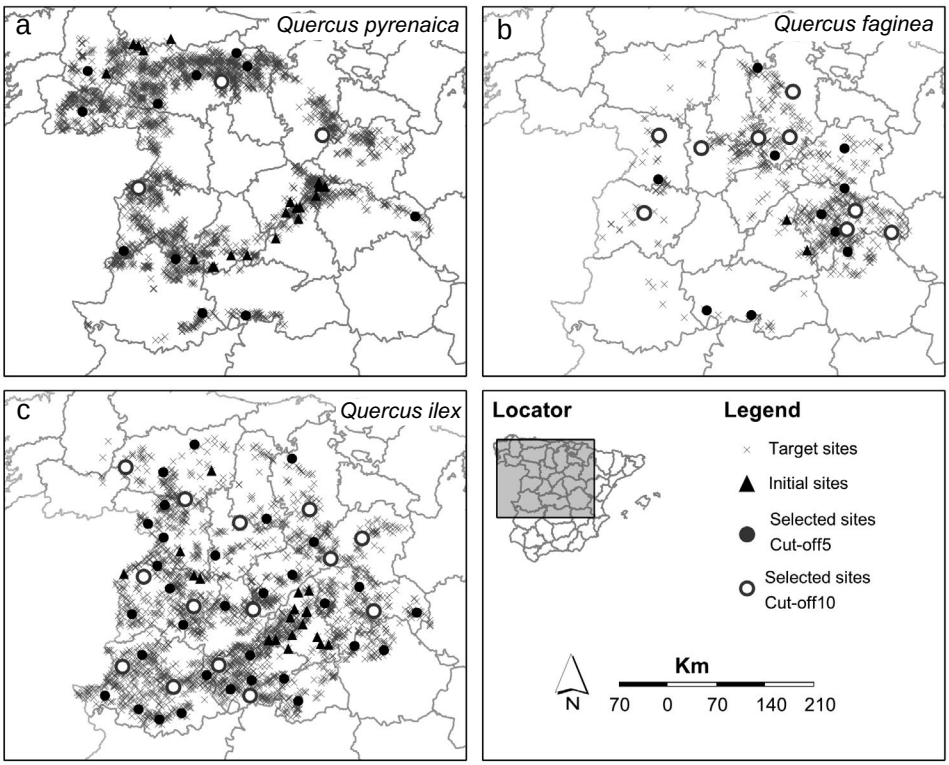

Figure 3.3: Distribution of the target, initial and selected sites for each forest type.

The distribution of *Quercus faginea* forests is centered in the mountainous region of the Iberian Mountain System that crosses the study area from northwest to southeast (Fig. 3.1). The variability within the study area was relatively low since this forest type has a comparatively narrow environmental (Table 3.1) and geographical range (Fig. 3.3b). The number of initial forests was very low (only 2 previously well known forests, Table 3.2, Fig. 3.3b). As a consequence, the initial percentage of uncovered variability was very high (*ca.* 50%, Fig. 3.4b). The first selected forests produced an outstanding decay in the uncovered variability so that the slope of the curve shows a steep decrease. Nine additional forests were necessary to achieve the cut-off10 level; at this point 24% of the geographic variability

and 34% of the environmental variability remained uncovered. Seventeen additional forests were necessary to achieve the cut-off5 level (Table 3.2); here, 16% of the geographic variability and 26% of the environmental variability will remain uncovered (Fig. 3.4b). At both cut-off levels the completeness of the inventory was above the 90% (Table 3.3).

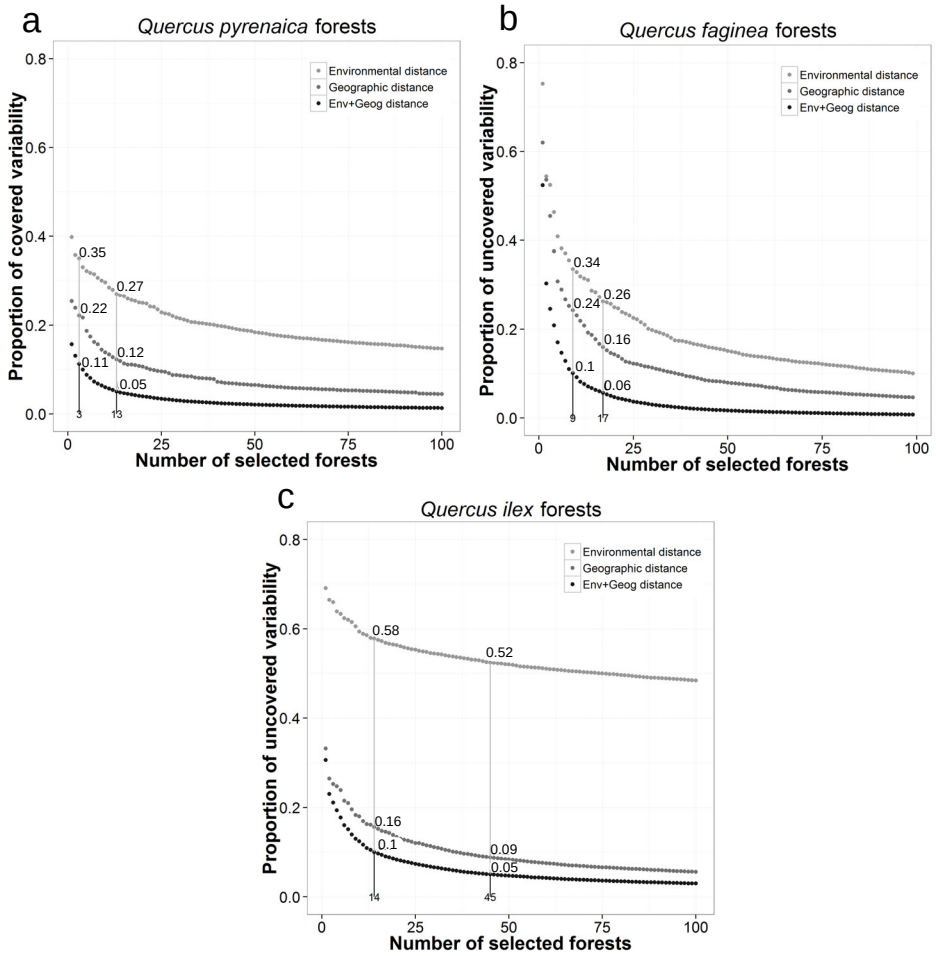

Figure 3.4: Decay in the proportion of uncovered variability after the selection of a new forest. Black lines show the cut-off levels for the combined matrix (including environmental and geographic distance). Vertical lines show the proportion of geographic and environmental variability not covered by the surveys.

Quercus ilex forests were the most abundant forest type within the study area and also the most variable both environmental and geographically. Although there was a high number of initial forests their distribution is clumped around the center of the study area (Table 3.2, Fig. 3.3c), so the initial figure of uncovered variability

was relatively high (30%, Fig. 3.4c). The decaying curve obtained is less steep than in the other two forest types. As a consequence, 14 forests were selected in order to attain the cut-off10 level. At this point although only 16% of the geographic variability remained uncovered, almost 60% of the environmental variability was yet to be covered by the sites selected for survey plus the already surveyed ones. In spite of the low level of coverage of the environmental variability, the inventory completeness was above 70% (Table 3.3). To attain the cut-off5 level 45 forests were necessary; here, the percentage of geographic variability uncovered was very low (below 10%) but the uncovered environmental variability still remained very high (above 50%) (Table 3.2 and Fig. 3.4c). At this level completeness was close to 90% (Table 3.3).

3.4 Discussion

Knowledge on biodiversity is scarce and suffers from collecting bias both at geographic and taxonomic levels (Rocchini *et al.* 2011; Ladle & Hortal 2013). Researchers usually focus their field campaigns in the most diverse or singular localities and tend to visit more frequently the most accessible sites (Hijmans *et al.* 2000; Kadmon, Farber & Danin 2004).

Forest type	n	Sobs	Sest	Q1	Q2	q0	g=1	g=Cut-off10	g=Cut-off5
Q. pyrenaica	1860	55	75	11	3	0.0059	4220	0.75	0.81
Q. faginea	511	33	36	6	5	0.0117	404	0.98	0.99
Q. ilex	622	62	86	14	4	0.0045	6235	0.72	0.88

Table 3.3: Estimated species richness at different survey efforts. n: number of samples already collected (note that we collected 20 samples in each forest); Sobs: observed species richness; Sest: estimated maximum species richness based on Chao2 estimator; Q1: number of singletons, Q2: number of doubletons; q0: the probability that the next sample contains a species that is new to the survey; g=1: the samples needed to collect all the estimated species. g=Cut-off10: an estimation of the percentage of the total species richness(Sobs/Sest) achieved when the uncovered variability of the environmental distance matrix equals 0.1. g=Cut-off5: an estimation of the percentage of the total species richness (Sobs/Sest) when the uncovered variability of the distance matrix equals 0.05

Besides, designing effective field surveys is hampered by the intrinsic complexity of biodiversity patterns. Here, we applied an ED-based protocol after Hortal &

Lobo (2005) that, taking into account the spatio-environmental variability and the previous collections, provides a framework to design effective, standardized and repeatable sampling campaigns. The results of our work in a region and group different from those of Hortal & Lobo (2005), show that the protocol can perform efficiently in most situations. The selected sites are representative of the biological diversity of the studied region and, at the same time, capture the environmental and spatial variability effectively. Even more, the desired levels of survey completeness are attained at an affordable sampling effort.

Advantages and opportunities

Differences and deficiencies in the geographic and environmental representation provided by the records that compose the known distribution of biodiversity may strongly bias the results of pattern analysis and compromise effective conservation planning (Dennis & Thomas 2000; Hijmans *et al.* 2000; Hortal & Lobo 2006; Hortal *et al.* 2007, 2008; Lobo 2008). One of the advantages of the *p*-median based protocol we applied is the possibility of controlling geographic and environmental representation by quantifying the amount of spatio-environmental variability covered. To test if the protocol was able to capture the spatio-environmental gradient efficiently we analyzed the three different scenarios provided by the three types of *Quercus*-dominated forests: *Q. pyrenaica* forests with medium spatio-environmental variability and a high number of initial sites; *Q. faginea* forests with restricted environmental and geographic distribution and just a few initial sites, and *Q. ilex* forests with very high spatio-environmental variability and a large number of initial sites. Our quantitative assessment showed that the selection of sites provided by the protocol produced a strong decay in the uncovered spatio-environmental variability, therefore effectively covering the analyzed gradient (Fig. 3.3). However, there were differences in the representativeness of the environmental and geographical spaces. In all three cases the geographic variability was recovered more effectively than the environmental variability. In *Q. pyrenaica* and *Q. faginea* forests the difference was small and the selection covered an adequate level of both spatial and environmental variability (uncovered variability always below 35%, see Fig. 3.4). In contrast, in *Q. ilex* forests the difference was very large, at cut-off10 only 16% of the geographic variability was uncovered, yet the uncovered environmental variability remained close to 60%. Even more, the decay of environmental distance stabilized close to 50% of uncovered variability. This may be caused by the low number of target sites compared to the large number of demand sites. *Q. ilex* forests have been subject to a long history of human

transformation (Costa, Morla & Sáinz 2005) and most of the remnants are highly disturbed patches in a fragmented landscape. As a consequence only 29% of the demand forests were sufficiently well preserved to be included as target sites. Therefore, recovering more than 50% of the environmental variability seems unfeasible. However, despite recovering such a low variability of the environmental matrix the protocol achieved high levels of completeness at both cut-off levels (78% and 88%), and therefore the results can be considered satisfactory taking into account the limitations in the availability of adequate sites.

Besides quantifying the variability covered by the survey it is also possible to control the relative importance of the environmental and geographic gradients by giving different weights to the environmental and geographical matrices before running the iterative algorithm (see step 1.4). This property enables controlling sampling intensity in the environment and geographic spaces separately. As a consequence, it makes possible adjusting the relative efforts in relation to the requirements of the study.

The protocol succeeded in capturing high levels of environmental diversity with a reasonable number of sampling points. *Quercus ilex* forests required the highest sampling effort. Nine additional forests were enough to achieve more than 70% of the estimated maximum richness. But a significantly higher effort (45 forests more) was necessary to rise above 80% of inventory completeness. While *Q. pyrenaica* forests required intermediate effort (see Tables 2 and 3), *Q. faginea* forests having lower diversity (both environmental and biological) achieved high completeness levels quickly. At the first cut-off level (9 additional forests) 95% of maximum biodiversity was achieved. Our work shows that for groups with high dispersal abilities a 10% of uncovered spatio-environmental variability is enough to recover a high percentage of the diversity in relatively long climatic gradients. Here, due to their high dispersal abilities bryophytes are known to have less steep accumulation curves (Ingerpuu *et al.* 2001; Peintinger *et al.* 2003) than groups with less vagile diaspores. This implies that each site is more singular in groups with lower dispersal abilities and therefore more sites are needed in order to achieve a good picture of the existing diversity. As a consequence the threshold recommended for groups with low dispersal abilities will be well over 10% of uncovered spatio-environmental variability. The same will be true for hyperdiverse taxa or very long gradients, here gathering exhaustive inventories will typically require recovering more than 90% of the spatio-environmental diversity.

One of the strengths of this technique lies on the possibility of getting feedback from the outcome of the sampling campaign (see Hortal & Lobo 2005). The

performance of the selection procedure can be tested by estimating the percent of recovered species richness over the expected maximum. If the evaluation is performed at early stages it is possible to calculate by extrapolation the effort needed to achieve the desired level. Because the process is iterative the researcher can easily include additional sites if necessary, following the order of selection.

A limitation to the applicability of this type of protocol is the apparent complexity of the procedure. However, the iterative part of the protocol (part 2) is implemented in an open source package on R (Medina & García 2010). This makes the most difficult steps fairly easy to apply. Additionally, in cases where the number of candidate sites is high, such as the one presented here, reviewing the characteristics of each of the forest patches and selecting them manually would have been by large more time-consuming than preparing the data and performing the protocol. That is, with the available resources performing the protocol is more a time-saving rather than a time-consuming task.

Challenges and limitations

The efficiency of ED procedures in maximizing the captured diversity has been challenged in the context of reserve selection, here the objective of the ED procedures is to recover the maximum diversity (Araújo *et al.* 2001; Hortal *et al.* 2009). However, when designing a field campaign the priority is not only to maximize collected richness but also to generate an unbiased and representative dataset that allows an accurate identification of the drivers of diversity patterns. In spite of their limitations, our results show that ED-based procedures are still useful to select representative samples and at the same time recover high levels of diversity. An important limitation of any ED-based protocol is related to the selection of the environmental variables. If we choose the wrong variables, it is quite likely that the protocol will perform inefficiently. Unfortunately, researchers only rarely have precise information on the primary drivers of species distributions (Hirzel & Guisan 2002). In fact, the objective of the sampling campaign will frequently be analyzing such patterns. So results based on partial knowledge of the environmental requirements of the species should be taken with care.

Besides, other effects apart from purely environmental drivers can modify species distributions and diversity patterns, making the protocol inefficient. Unconsidered effects (e.g. historic, biotic, anthropic) may produce higher variation than expected and provoke the effort needed to effectively sampling diversity to be

higher than predicted by the protocol. Including a measure of geographical distance in the protocol partially overcomes this problem. As we have proven, this can be a sound and practical strategy even for organisms with high dispersal abilities such as bryophytes; therefore including geographic space is always recommended. Unfortunately, other sources of bias may be even more difficult to control. If uncertainty regarding the diversity patterns is high, it is advisable to control the efficiency of the protocol in capturing diversity. Finally, the performance of the protocol is strongly influenced by the initial sites. This is an advantage when there is a set of previously known localities as it allows finding the complementary ones. However, it can be a problem when there are no previously well known sites. In such cases the initial sites have to be set at random. To minimize the possible dependence on the initial selection the protocol should be tried with several sets of initials and the selections should be weighted by the frequency of selecting each target site.

3.5 Concluding remarks

Designing efficient sampling strategies is crucial for pattern analysis, modeling and conservation policies. The decision of what localities to sample and the intensity of the sampling effort are of paramount importance since the outcome of the study and the reliability of the results will be affected by those decisions. The applied protocol proved to be a useful tool to locate selection sites and establish sampling intensity in a standardized and repeatable way. Also, it i) minimizes time consumption during the selection process; ii) maximizes the spatio-environmental diversity covered; iii) allows quantifying the covered percentage of environmental and geographical space; and iv) helps to select adequate levels of sampling effort with objective criteria. Therefore, the ED-based selection protocol proposed by Hortal & Lobo (2005) provides a repeatable and effective method to select sampling sites.

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CHAPTER

4

Data paper: Epiphytic bryophytes of *Quercus* forests in Central and North inland Iberian Peninsula

Abstract

Diversity patterns are governed by a complex network of interacting factors. Studies directed to disentangle the most important factors affecting diversity have frequently shown divergent results, which has encouraged a rewarding debate about the relative importance of each factor. Scale dependency has been identified as a direct cause of at least part of such divergences. However, studies with spatially-explicit measurements at different scales are costly and therefore they are relatively scarce despite their importance. Here, we present a database to disentangle the cross-scale variation in the importance of factors affecting the diversity of epiphytic bryophyte communities in *Quercus* dominated forests (*Quercus ilex* L., *Quercus pyrenaica* Willd. and *Quercus faginea* Lam. in the North-western region of the Iberian Peninsula. We provide species-per-site abundance information with more than 9000 entries and an environmental table containing 20 *in situ* measured variables at three different scales (forest, stand, and sample). The database will help to advance the research of cross-scale effects of diversity patterns while at the same time providing valuable information on the distribution of a poorly known group of organisms.

4.1 Introduction

The whys and wherefores of the distribution of biodiversity in space have long intrigued ecologists (Elton 1946; Hutchinson 1959), and are still the source of debate(see e.g. Kraft *et al.* 2011). Currently we hold much knowledge on the causes of biodiversity gradients. For example, current climate is known to constrain species richness patterns (Hawkins, Porter & Diniz-Filho 2003), at least to some extent (see Hortal *et al.* 2011). However, there is a lack of consensus on many aspects of the relationships between biodiversity and a number of other factors, and the underlying mechanisms driving diversity patterns are still under discussion (see for example, current debate on the relationship between net productivity and diversity in Gillman *et al.* 2014). In addition, the relative importance of each factor has also been the subject of continuous debate (Ricklefs 2008; Brooker *et al.* 2009). Allegedly, at least part of the controversy is related to the scale dependency of diversity patterns (Willis & Whittaker 2002). Although the importance of cross-scale effects has been long recognized, only recently has it become a key question in biodiversity studies (Whittaker, Willis & Field 2001; Hortal *et al.* 2010; Guisan & Rahbek 2011). However, acquiring standardized data at multiple scales is usually cost-intensive, so the number of studies dealing with cross-scale changes in the drivers of diversity is relatively scarce. Therefore, there is an urgent need for reliable, spatially-explicit data that provides information on the variations of diversity across scales.

The relative significance of the factors affecting diversity patterns and the scale at which they become apparent depends on the ecology and life history of the taxa under consideration (Whittaker *et al.* 2001). Recently there has been an increase in the taxonomic scope covered by biodiversity studies that has begun to clarify the relationship between biodiversity patterns and the life history traits of the organisms under study (Diniz-Filho, De Marco Jr & Hawkins 2010; Heino 2011; Santos & Quicke 2011; Aranda *et al.* 2013; Patiño *et al.* 2014). However, an important gap of knowledge still remains (e.g. Fontaneto & Hortal 2013). As for many other small-sized, inconspicuous taxa, knowledge on the diversity patterns of bryophytes is scarce (Medina, Draper & Lara 2011). Interestingly, they have unique characteristics that make them an ideal study system to test hypotheses related to changes in the factors affecting biodiversity across scales. Because of their small size and their ability to be in thermic and hydric equilibrium with the environment they are thought to be strongly dependent on the immediate (micro-scale) environment, whereas at the same time they are also known to depend on general meso-climatic

conditions. Within bryophytes, epiphytes in Mediterranean forests are particularly well suited to analyse cross-scale relationships because they grow in a set of nested island-like systems: at the landscape-scale forests are isolated patches in an unsuitable matrix while at the smallest scale trees are islands in a mostly unsuitable area (see Medina *et al.* 2014).

Here we present data designed to disentangle the cross-scale variation in the importance of the factors affecting the diversity of epiphytic bryophytes. To do so we surveyed epiphytic bryophyte communities in *Quercus* dominated forest (*Quercus ilex* L., *Quercus pyrenaica* Willd. and *Quercus faginea* Lam. at three different scales (forest, stand, and sample), using a standard protocol to avoid including eventual variations in community structure within each individual tree. More precisely, we describe the sampling strategy and the obtained output, providing spatially-explicit data on species composition and environmental conditions at the three scales of analysis.

4.2 Materials and Methods

Study area

The surveys spanned North and Centre Inland Spain, encompassing an area of *ca.* 150,000 km^2 (Fig. 4.1). This region covers a wide climatic gradient with large variations in precipitation and temperature regimes. In the north of the study area (Fig. 4.1) climate is predominantly Atlantic with a characteristic humid to very humid summer and relatively mild temperatures. The rest of the territory hosts several variants of the Mediterranean climate that can be separated into three different regions (Mediterranean, Continental and Mediterranean-Atlantic) that show large differences in the temperature regime, season of maximum precipitations and intensity of summer drought. The study area covers a small part of the area under Atlantic climate and the continental region within the area under Mediterranean climate. Within the continental region there is also an important climatic variation. The westernmost zone of the study area in the border with Portugal is within the mild continental zone (Fig. 4.1). Due to the influence of the Atlantic Ocean, this zone shows rainy winters with infrequent snows and less than 40 frost days, that become even less towards the south. The inner part of the study (continental zone, Fig. 4.1) area has wider temperature variations, with most precipitations occurring during spring or autumn.

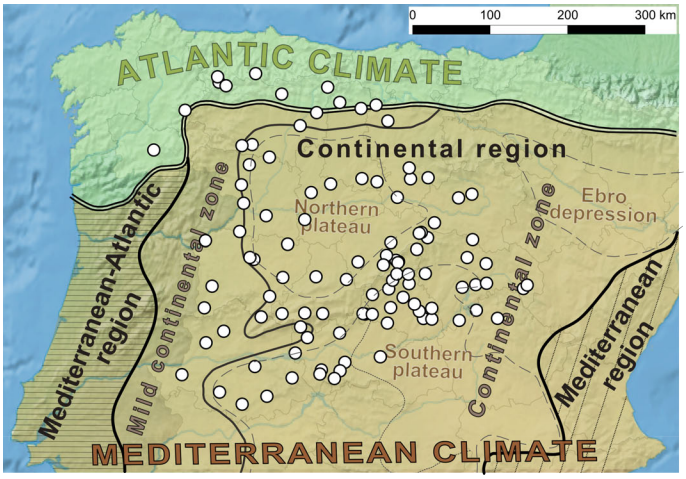

Figure 4.1: Map depicting the climatic regions of the study area, modified after Tullot (2000). White dots show the location of the sampled forests

Within the continental zone the study area shows three well-differentiated units that stands out because of their singular climatic conditions. The northern plateau (Fig. 4.1) is an elevated plain surrounded by mountains. Its distinctive characteristics include cold winters (with locations that bear up to 170 frost days in the easternmost facade) and warm summers. Precipitations are low (less than 500 mm per year in most of this zone) and despite the ample daily temperature variations dew is relatively uncommon due to the low air humidity. The southern plateau (Fig. 4.1) is less isolated and has a higher topographic complexity, thus harbouring more heterogeneous conditions. Overall, the southern plateau has warmer winters and hotter summers but, most importantly, this region is characterized by a longer and dryer summer drought, especially in the western half of the plateau that bears the hardest conditions. The third unit is comprised by mountainous areas surrounding the plateaus (Fig. 4.1). Overall, these mountain ranges represent wet and relatively cold areas. However, they harbour a highly diverse mosaic of climatic conditions due to their topographic complexity, where the relief and orientation play a paramount role shaping temperature and precipitation regimes.

Survey design

The selection of the sites to be surveyed was directed to obtain a good representation of the climatic and spatial variability of the study area. We based the selection procedure on a *p*-median Environmental Diversity protocol (Hortal & Lobo 2005),

designed to maximize the environmental variability covered by the surveys, taking also into account previously-known localities(see N.G. Medina *et al.* 2013 for a complete description of the selection method).

We sampled 107 forests. Forty of these forests had previous information on species composition and abundance at the forest scale (Lara 1993; Albertos *et al.* 2005; Cortés 2005), while the remaining 67 forests were sampled during the current survey and therefore have detailed information on species composition and abundance at the three scales of analysis (forest, stand, and sample; see below).

Sampling method

Environmental characteristics were recorded at three scales of analysis in all the 107 forests. The strategy followed to sample the three scales of analysis is summarized in Fig. 4.2. We first examined aerial photographs and traversed the forest to locate and select three stands separated by at least 100 m that had homogeneous conditions and where representative of the overall structure of the forest (Fig. 4.2a). Then we established the centre of the stand in an area more or less equidistant to the closest trees (Fig. 4.2b). Stand-scale characteristics were measured on the circular plot that included the 6 closest trees to the centre. Finally, we divided the stand into 4 sectors using the geographic North as reference, and made a division every 45 degrees (Fig. 4.2b). Micro-scale characteristics were measured on the tree that was closest to the centre in each of the four sectors.

Several sampling strategies can be used to survey epiphytic bryophyte communities. Some studies use sampling units of fixed size and sample all the trees in each unit (Király & Ódor 2010; Király *et al.* 2013; Ódor *et al.* 2013). However, this method is unpractical in Mediterranean environments, especially in forests under strong anthropic influence. In these conditions, tree density is highly variable and there can be large differences in the number of trees per sampling unit. Therefore, if a quadrat of fixed size is used, some units will have just one tree –leading to a clear underestimation of epiphyte richness– while other sampling units will have an unpractically high number of samples. Because of this, our approach is based on using a fixed number of samples. This strategy is the most common approach in the study of epiphytic bryophytes in Mediterranean environments (see e.g. Lara 1993; González-Mancebo *et al.* 2004; Albertos *et al.* 2005; Garcia, Sérgio & Sim-Sim 2005; Draper *et al.* 2006; Ezer, Kara & Düzenli 2009; Mazimpaka *et al.* 2010)

Twenty samples were collected in each forest, which is known to be enough to obtain an adequate representation of the diversity of epiphytic bryophytes in

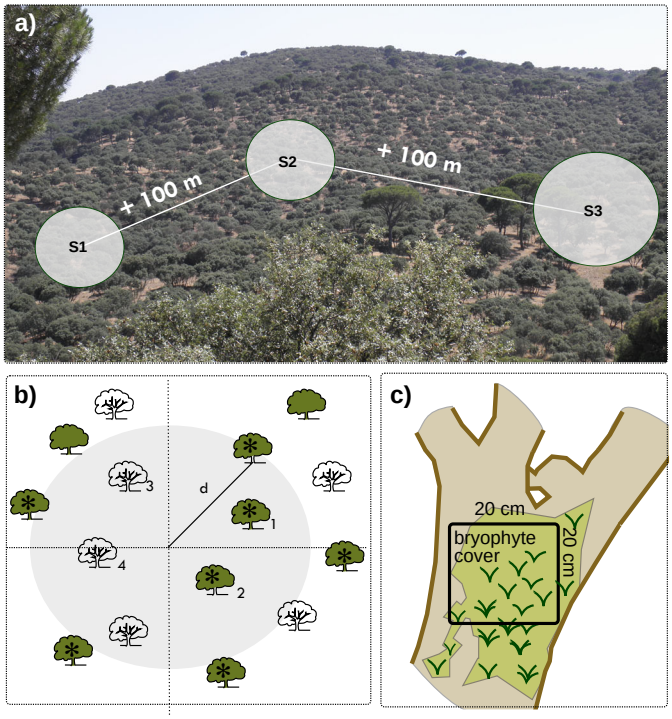

Figure 4.2: Scheme summarizing the sampling strategy at the three scales of analysis. a) S1, S2 and S3 refer to the three stands surveyed in each locality. b) The numbers indicate the trees were the environmental measures at the tree scale were taken, whereas *d* is the diameter to the sixth closest tree to the centre. Green coloured trees represent trees colonized by bryophytes and stars indicate sampled trees. c) The black quadrat depicts the sampling area in each tree

Mediterranean environments (Lara 1993; Albertos *et al.* 2005; Mazimpaka *et al.* 2010; Medina *et al.* 2010, 2014). We collected seven samples in the first two stands and six in the last one. The proportion of trees colonized by bryophytes varied from all or most tree trunks in some forests, to less than 10% in others. In the cases were the proportion of colonized trees was low, we established a stopping rule to avoid overlapping areas across stands. Thus we stopped searching for trees after visiting 100 trees in a forest (35 visited trees in the first two stands and 30 trees in the last one).

For each sampled tree trunk we took samples at a height between 1.20 m and 2.00 m above the ground (Fig. 4.2c). Such height avoids an excessive influence of the colonization of soil bryophytes while providing relatively similar conditions of humidity across the forest, thus ensuring that the sampled communities are mainly composed of typically epiphytic bryophytes and that the samples are comparable.

Each sample consisted of a quadrat of 400 cm^2 in the side of the tree with the highest bryophyte cover. At each quadrat, bryophyte cover was estimated visually and then all bryophytes within the quadrat were collected. All species were identified based on specialized literature (Pedrotti 2001; Casas *et al.* 2006, 2009; Guerra, Cano & Ros 2006; Guerra *et al.* 2010; Guerra, Cano & Brugués 2014; Brugués, Cros & Guerra 2007). Nomenclature follows Ros *et al.* (2007)for liverworts and Ros *et al.* (2013) for mosses, except for *Orthotrichum comosum*, which was described after this latter checklist (R. Medina *et al.* 2013). Vascular plants are according to Castroviejo (1986).

Data description

The database consists of a compressed file in RAR format and two separate CSV files and a text file The compressed file (*SpDistr,* includes the distribution maps of the species found in the study area in a PNG format and a description of the most common distribution types that can be found in the study area in a text file (*DistrType*). The distributions of the species are also available in the appendix section (Figs B1 to B4) todether with the description of the distribution types Appendix B.1. The first CSV file contains data on species occurrences and their abundance (*spabun*), the other CSV file includes the rest of the variables (*var*), and the text file describes the data type and units of the columns in the *var* file. In both CSV files the first column (*Loc*) indicates the locality number, the next one (*Stand*) indicates the number of stand (S0 for the data coming from previous surveys where species occurrences were recorded only at the forest and sample scales and S1, S2 or S3 refer to the first, second and third stand of the data acquired in this study), and the third one (*Sample*) identifies each sample with a unique code. Missing data are encoded as NA (Not Available). In the species database, the remaining columns depict the abundances of the 88 species of bryophytes found during the surveys, measured as the percentage of the 400 cm^2 sample occupied by the species.

In the environmental database the first column after *Sample* is called *Source* and identifies the origin of the data: 0 present study, 1 data collected in Lara (1993), 2 data collected in Albertos (2001) and 3 collected in Cortés (2005). The next columns refer to the variables as described below:

Data at the forest scale: The database includes several geographic references of the localities including Province *(Prov)* and Town *(Town)*, as well as the geographic coordinates *(CoordX and CoordY,* datum WGS84*)*. This information is followed by a date column *(Date)* and topographic data gathered in the field: altitude *(Alt)* was

measured with a GPS, aspect *(Aspect)* was measured with a compass (stands in flat surfaces are coded as "F" to avoid confusion with North aspect, 0 degrees) and slope *(Slope)* was visually estimated. The database also includes information on the type of forest *(ForTyp)*, a categorical variable with three levels: QI for the forests dominated by *Quercus ilex*, QF for the forests dominated by *Q. faginea* and QP for the forests dominated by *Q. pyrenaica*. Finally at the forest scale we included a variable related to forests and landscape structure forest history *(ForH)* that is available only for *Quercus ilex* dominated forests and accounts for changes in forest structure in the last 57 years. To classify the forests we compared aerial photographs taken nowadays to the ones taken in a flight from the 1956 to 1957 American flight [1]. We grouped the forests into three categories: (1) "forested" if the forest had a similar structure in 1956-57 than nowadays, (2) "degraded" if the forest had a more open or degraded structure in 1956-57 and (3) "strongly degraded" if the forest had a very opened or shrub-like structure in 1956-57.

Data at the stand scale: At this scale we recorded several variables that describe forest structure. Canopy cover (*CanCov*) is defined as the proportion of the forest floor covered by the vertical projection of the canopy (Jennings, Brown & Sheil 1999). It was visually estimated in the field taking the surface of each stand as a reference (see stand area definition in Fig. 4.2b). Tree density (*TrDens*) was estimated by applying the formula:

$N(trees/ha) = \frac{10{,}000*5.5}{\pi*d}$

where d is the distance to the sixth closest tree to the centre of the stand (Fig. 4.2b). The average diameter of the trees in a stand (*ForDiam)* was calculated as the mean of the diameters at breast height of the six trees located closer to the centre of the stand. Tree species (*TrSp)* is a complex variable that details the scientific names of the tree species found in the stand followed by their importance (an estimation of the percentage of trees of each species in the stand). Additionally, we also estimated shrub cover (*ShrubCov*)as the percentage of the forest floor occupied by shrubs, as well as their average height in meters (*ShrubHeig*). Finally, we included a variable related to the percent of trees that were colonized by bryophytes (*PerCol).*

Data at the sample (tree) scale: At this scale we measured several variables that are known to be representative of the variation of the tree scale micro-environment and at the same time have proven to be relevant for the diversity and structure of bryophyte communities. Bark roughness *(BarkRough)* was estimated as the

[1] http://www2.ign.es/iberpix/visoriberpix/visorign.html last accessed 27/11/2014

average depth of two furrows, namely the two deepest ones at breast height in each of two sides of the tree. The diameter (*Diam*) at breast height (1.50 m) was measured with a *DendroFlexómetro*© that uses a Biltmore scale to correct for the curvature of the tree surface. Note that this is different to the measure the average diameter at the stand scale (*ForDiam*), as this *Diam* is based on the four trees that are closer to the centre in each of the four sectors, while the *ForDiam* is based on the six trees located closer to the centre irrespective of their orientation (Fig. 4.2b). Canopy depth (*CanDep*) was calculated by subtracting the total height of the tree to the height at which the crown starts. Height was calculated using a DendroFlexómetro© that has a Christen scale incorporated. Additionally, we measured two indicators of the amount of light that passes through the canopy (*LAI1* and *LAI2*). To calculate them we took two hemispherical photographs of the canopy at 1m height and a distance of 50 cm from the trunk surface at the North and South faces of each tree with an Olympus SP590-UZ camera and a fisheye lens. Then we estimated the percent of sky covered by the canopy *(LAI1)* and the total amount of light that passes through the canopy *(LAI2)* with GLA software (Frazer, Canham & Lertzman 1999). LAI2 was calculated taking into account the geographic position, cloudiness (*kt*), spectral fraction (*sf*), beam fraction (*bf*) and topography of the site. Data on *bf* for each site were extracted from PGIVS maps, and *kt* and *sf* were derived from *bf* using the formulae on GLA user manual (Frazer *et al.* 1999). Here note that both LAI indices refer to the mean amount of light per day taking into account all the year for the perennial species (*Quercus ilex*), while for the deciduous species (*Quercus pyrenaica* and *Quercus faginea*) this amount of light corresponds to the period of the year when those species remain with leaves. The total number of days was calculated based on the known phenology of these species in the Iberian Peninsula. Finally, we included two variables related to biotic characteristics: the percentage of the quadrat of 400 cm^2 that is occupied by bryophytes *(BrioCov)* and lichens *(Liq)*, estimated visually in the field in both cases.

4.3 Data overview and relevance

Overall, the database holds more than 9000 entries from 88 species of mosses and liverworts. Both bryophyte diversity (see distribution maps, Supplementary Material S1) and environmental characteristics (Fig. 4.3) vary widely among forests.

The data presented here offer the opportunity to explore several ecological questions. On the one hand, we provide spatially-explicit data at three different scales that allow exploring the hierarchies of variables that affect species diversity,

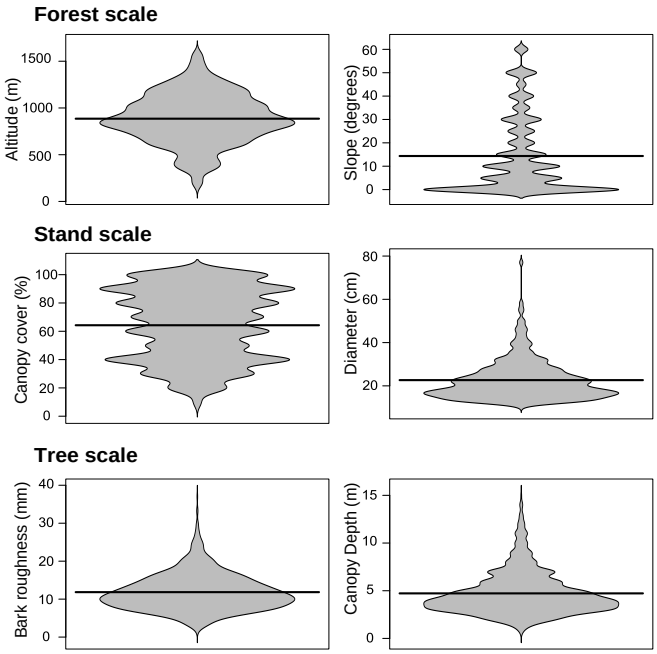

Figure 4.3: Beanplots of the quantitative variables in the database. We have selected two variables per scale to illustrate the variability across forests. Grey area represents the area under the density curves of the data values; the horizontal line is the average value

as well as the relative importance across scales of the different factors determining both richness and changes in community composition. In addition, the information included in this database makes possible to explore distribution patterns of the species at different scales and to test to what extent occurrence data are constrained by species distributions at higher levels. The database offers a plethora of environmental measures that can be used not only for bryophyte studies, but also for other studies relating forest structure with diversity. Apart from its relevance to evaluate general ecological questions, these data also expands the knowledge on the distribution of bryophytes. The database presented here is the outcome of a systematic study covering the northern plateau and part of the southern plateau of the Iberian Peninsula, an area that has been scarcely visited by bryologists. We therefore expect these data to be used for ecological studies, checklists and distributional atlases, helping to unveil the determinants of the structure of local epiphytic bryophyte communities and the distribution of bryophyte species.

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CHAPTER

5

Catálogo de los briófitos epífitos que crecen en bosques de quercíneas del cuadrante noroccidental ibérico

Resumen En las últimas décadas se han producido importantes avances en el conocimiento de la brioflora ibérica. En este sentido se puede decir que la brioflora ibérica se conoce relativamente a nivel taxonómico. Sin embargo, en cuanto a las distribuciones de las especies aun queda mucho trabajo por hacer. La mayor parte de los estudios se han centrado en zonas montanas y/o singulares o bien en los entornos de las residencias de los especialistas. Esto ha producido un un importante sesgo en el conocimiento de las distribuciones que es necesario solventar realizando estudios sistemáticos centrados en conseguir una muestra representativa de los principales gradientes ambientales y geográficos de la Península. Precisamente, el objetivo del presente trabajo es contribuir a reducir de forma significativa las lagunas en el conocimiento de la distribución de los briófitos epífitos ibéricos. Para ello, se ha estudiado buena parte de las mesetas centrales incluyendo las porciones españolas de las cuencas del Duero y del Tajo, dos de las regiones menos exploradas de la Península Ibérica. El catálogo incluye 89 especies de briófitos entre las que hay 9 hepáticas y 80 musgos. El presente estudio aporta además 72 nuevas citas provinciales y amplía significativamente la distribución conocida de un buen número de especies. Queda patente la importancia de llevar a cabo muestreos sistemáticos representativos de los gradientes ambientales y geográficos en zonas poco exploradas de modo que se vayan rellenando los huecos en el conocimiento de las distribuciones de los briófitos ibéricos.

5.1 Introducción

El conocimiento sobre los briófitos de la Península Ibérica ha experimentado un espectacular progreso en los últimos 40-50 años, en buena medida gracias a que tanto España como Portugal cuentan con un alto número de grupos activos especializados en Briología (Infante 2005). En este contexto, la publicación de la Flora Briofítica Ibérica (`http://www.florabriofiticaiberica.com`) ha supuesto un importante avance a la hora de completar el conocimiento de los briófitos peninsulares, de tal modo que actualmente puede considerarse que, a nivel taxonómico, los musgos ibéricos se conocen relativamente bien. Sin embargo, en cuanto a la distribución y abundancia de las especies, el conocimiento es mucho más limitado (Lara *et al.* 2005). A pesar de los avances realizados hasta la fecha, la Península Ibérica continúa siendo una región poco explorada desde el punto de vista briológico, especialmente si la comparamos con las áreas europeas mejor conocidas, como es el caso de las islas británicas (Blockeel *et al.* 2014). Una de las limitaciones más importantes en el conocimiento de la distribución de las especies está relacionada con el sesgo espacial en el esfuerzo de muestreo (Aranda *et al.* 2010; N.G. Medina *et al.*, 2013). Así, la mayor intensidad de herborización se concentra en zonas montanas y/o singulares o bien en los entornos de las residencias de los especialistas. Mientras, las zonas basales acumulan importantes lagunas ya que resultan menos atractivas, bien porque las condiciones son más homogéneas o bien porque la acción antrópica ha sido más intensa en estas áreas.

Los briófitos epífitos quizás ejemplifican bien esta parcialidad en el conocimiento. En la Península Ibérica en los últimos 20 años se ha realizado un buen número estudios sistemáticos centrados en la descripción de las comunidades de briófitos epífitos (Lara 1993; Albertos 2001; Calleja *et al.* 2001; Garcia 2006; Medina *et al.*, 2010). Hay también algunos otros trabajos que, sin ser específicos de briófitos epífitos, han aportado contribuciones significativas al conocimiento de su distribución (por ejemplo García-Zamora, Ros & Guerra 2000; Rams 2007; Cezón & Muñoz 2013), así como muchos otros de ámbito más local. Aunque *a priori* pudiera parecer que el número de estudios es alto, lo cierto es que al analizar en detalle el ámbito geográfico al que se refieren, se constata que prácticamente todos se centran en áreas montañosas. De modo que si se quiere completar las lagunas en el conocimiento hay que comenzar por realizar trabajos que recojan de forma sistemática la variación geográfica y ambiental de zonas amplias, estudios que incluyan tanto áreas montanas como zonas basales. El objetivo del presente trabajo es, precisamente, contribuir a reducir de forma significativa las lagunas en el conocimiento

de la distribución de los briófitos epífitos ibéricos. Para ello, se ha estudiado un área amplia, que abarca buena parte de las mesetas centrales y que se extiende, más en concreto, por las porciones españolas de las cuencas del Duero y del Tajo, dos de las regiones menos exploradas de la Península Ibérica.

5.2 Material y métodos

El presente catálogo se basa fundamentalmente en una serie de muestreos realizados entre 2008 y 2013. Con las recolecciones se pretendía conseguir una muestra representativa de la variabilidad florística condicionada por los gradientes ambientales y geográficos en el área de estudio. Por ello, se realizó una selección de localidades basada en un algoritmo de optimización a partir de distancias ambientales denominado *p*-median; (la descripción detallada del método de selección se puede encontrar en N.G. Medina *et al.*, 2013). En total se incluyeron 107 bosques (Anexo C) entre los que además de los muestreados realizados *ex profeso* para el estudio, se incluyeron una selección de localidades previamente estudiadas por nuestro equipo de investigación en el mismo entorno geográfico: 6 bosques seleccionados del área estudiada por Albertos (2001); 14 bosques de los incluidos en Cortés (2005); 14 bosques de los estudiados por Lara (1993). En cada localidad se tomaron sendas muestras en 20 árboles siempre que fue posible. Las muestras se recolectaron en troncos a una altura de entre 1,20 y 2 metros.

A continuación se relacionan las especies de hepáticas y de musgos censadas, las cuales se disponen en orden alfabético, separando hepáticas y musgos. Para cada taxón se indica: a) las localidades en las que ha aparecido, ordenadas por provincia, señalándose con un asterisco (*) las novedades provinciales; b) una breve descripción de la distribución en el área de estudio y la abundancia con la que aparece la especie, estimada a partir del índice de abundancia IES (Lara & Mazimpaka 1998; Albertos *et al.* 2001a) (Tabla 5.1): IES = F (1+C). Donde F es la frecuencia relativa en tanto por cien y C es la cobertura media ($\sum$ Ci/x), siendo x el número de muestras que contienen una especie dada la cobertura de la especie agrupada en clases. Los adjetivos que expresan los niveles de abundancia de cada especie se refieren siempre a los valores de abundancia obtenidos (índice IES), según los intervalos expresados en la Tabla 5.1 (Albertos 2001)

Con el objetivo de facilitar la interpretación de las descripciones de este apartado se han representado las distribuciones y abundancias de las especies más difundidas (Figs. 5.1 a 5.6). Se ha optado por representar, de manera general, aquellas

Abundancia	Valor de IES
Muy escaso	<20
Escaso	20-59
Moderadamente abundante	60-149
Abundante	150-299
Muy abundante	≥300

Tabla 5.1: Equivalencias de los niveles de abundancia y los valores de IES

con más de 6 localidades en el área de estudio y, excepcionalmente, otras especies que aun habiendo aparecido menos, tienen una distribución compleja o con los niveles de abundancia muy cambiantes.

La nomenclatura sigue a *Ros et al.* (2013) para los musgos y *Ros et al.* (2007) para las hepáticas. Para las plantas vasculares se sigue a Flora Ibérica (Castroviejo 1986). Se ha depositado un pliego testigo de cada especie hallada en cada localidad en el herbario de la Universidad Autónoma de Madrid (MAUAM).

Es necesario advertir que el catálogo recoge tan sólo los briófitos que habitan en las circunstancias ecológicas concretas analizadas en el estudio: troncos de árboles de edad intermedia, pertenecientes a las especies que dominan los encinares, melojares y quejigares (*Quercus ilex* subsp. *ballota*, *Q. pyrenaica*, *Q. faginea*, respectivamente). De esta manera, especies que en un área determinada son comunes en las bases de los árboles, sobre los troncos muy viejos o sobre otras especies de forófitos, pueden no estar presentes o mostrar abundancias reducidas en las localidades y condiciones que aquí se estudian.

5.3 Catálogo florístico

Hepáticas

***Frullania dilatata* (L.) Dumort.** – Asturias: 1, 2, 3, 4; Ávila:8, 9; Burgos: 13, 14, 15, 16; Cáceres: 20, 22, 24; Guadalajara: 29, 32, 33, 34; León: 42, 43, 47; Lugo: 48; Madrid: 52, 56, 58, 59, 60, 61, 64, 67; Orense: 68; Palencia: 69, 72; Salamanca: 74, 77, 79, 81; Segovia: 83, 84; Toledo: 94, 95, 96, 98, 99; Zamora: 105, 106, 107. Casi exclusivamente en las zonas montañosas del área de estudio. Especialmente frecuente en la Cordillera Cantábrica y en el Sistema Central y su entorno, más esporádica en los Montes de Toledo y el Sistema Ibérico. Abundante a muy abundante en los robledales del noroeste del área de estudio y en los melojares

y algunos encinares de la porción occidental del Sistema Central; muy escasa a escasa en el resto de las localidades (Fig. 5.1a).

Esta hepática se había citado previamente de una sola localidad en las provincias de Palencia (Fuertes *et al.* 1998) y Toledo (Allorge 1946).

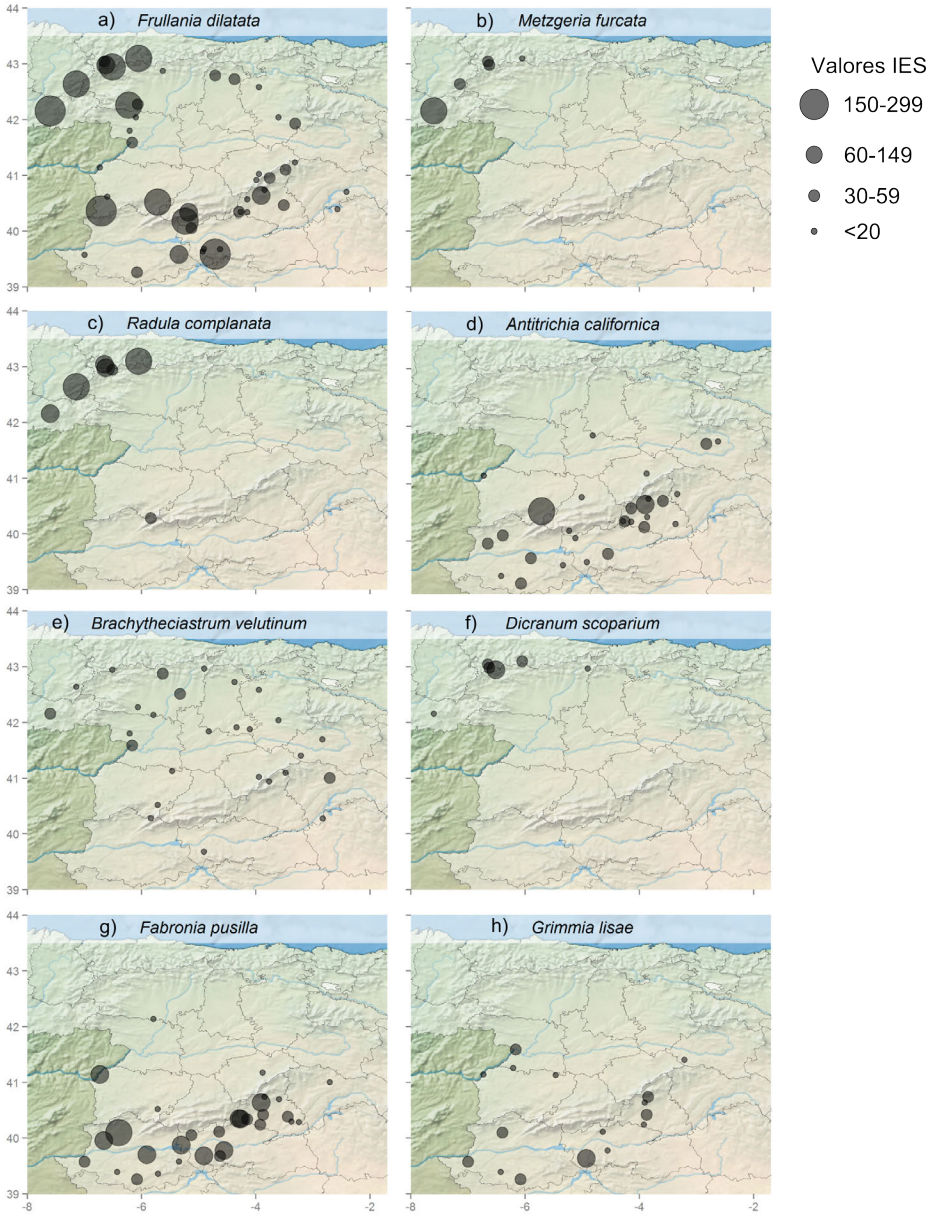

Figura 5.1: Mapas de distribución de algunas especies de briófitos epífitos recogidas en el catálogo. El tamaño de punto expresa la abundancia medida por medio del IES

***Frullania microphylla* (Gottsche) Pearson** – Asturias: 3. En un robledal, escasa.

***Frullania tamarisci* (L.) Dumort.** – Asturias: 1, 2, 3, 4; Lugo: 48; Orense: 68. Restringida a los robledales del noroeste del área de estudio. De muy escasa a abundante según las localidades.

***Lejeunea lamacerina* (Steph.) Schiffn.** – Asturias: 3. En un robledal, muy escasa.

***Metzgeria violacea* (Ach.) Dumort.** – Asturias: 1. En un robledal, muy escasa

***Metzgeria furcata* (L.) Dumort.** – Asturias: 1, 2, 3; Lugo: 48; Orense: 68. Restringida a los robledales del extremo noroeste del área de estudio. Muy escasa o escasa, salvo en la localidad 68, donde es abundante (Fig. 5.1b).

***Porella obtusata* (Taylor) Trevis.** – Asturias: 1. En un robledal, muy escasa.

***Porella platyphylla* (L.) Pfeiff.** – Ávila: 9; León: 43; Segovia: 83, 86. Ocasional en melojares de la cara norte del Sistema Central y en un encinar de la Cordillera Cantábrica. Muy escasa o, excepcionalmente, escasa.

***Radula complanata* (L.) Dumort.** – Asturias: 1, 2, 3, 4; Cáceres: 25; Lugo: 48; Orense: 68. Común en robledales del noroeste del territorio y ocasional en los del Sistema Central. De escasa a abundante, con los valores más altos en la Cordillera Cantábrica (Fig. 5.1c).

Musgos

***Alleniella complanata* (Hedw.) S.Olsson, Enroth & D.Quandt** - Asturias: 3; Lugo: 48; Palencia: 69, 70. Presente tan sólo en el norte del área de estudio, es escaso en los melojares de Asturias y Lugo y muy escaso en las localidades Palentinas.

***Antitrichia californica* Sull.** – Ávila: 5, 8; Cáceres: 18, 20, 23, 24, 26; Guadalajara: 40; Madrid: 49, 52, 53, 54, 56, 57, 58, 59, 60, 67; Salamanca: 74, 77; Segovia: 85; Soria: 90, 91; Toledo: 93, 96, 99; Valladolid*: 101. Este musgo ha aparecido casi exclusivamente en encinares (tan sólo en un melojar del área carpetana). Se encuentra principalmente en el piedemonte del Sistema Central, donde suele ser escaso, aunque localmente llega a valores de abundante o muy abundante (localidades 52 y 77 respectivamente). Es escaso o muy escaso, aunque no infrecuente, en encinares del Sistema Ibérico septentrional, Montes de Toledo y de la meseta Sur. En la meseta Norte es muy poco común y solo se ha encontrado, muy escaso, en algunas localidades (Fig. 5.1e).

***Antitrichia curtipendula* (Hedw.) Brid.** – Asturias: 2, 3, 4; León: 46, 47; Lugo: 48. Solamente en los melojares de las áreas montanas del noroeste del área de estudio, donde es escaso o muy escaso, salvo en las localidades asturianas 2 y 3, en las que resulta moderadamente abundante.

***Bartramia rosamrosae* Damayanti, J. Muñoz, J.-P. Frahm & D. Quandt** – Cáceres: 22. En un encinar, muy escaso.

***Brachytheciastrum velutinum* Ignatov & Huttunen** – Asturias: 4; Burgos: 14, 15; Cáceres: 25; Guadalajara: 33, 35, 38; León: 41, 42, 43, 44, 46; Lugo: 48; Madrid: 63; Orense: 68; Palencia: 69, 71, 73; Salamanca: 76, 77; Segovia: 83; Soria: 89, 90; Toledo: 95; Valladolid*: 101; Zamora: 105, 106. Distribuido principalmente en los encinares de la meseta Norte, también presente en melojares del Sistema Central y del noroeste del área de estudio. Ocasional en encinares al sur del Tajo. Muy escaso o escaso en todo el territorio.

Casi todas las muestras corresponden a la variedad *velutinum*; sólo los materiales de la localidad 15 (Burgos) corresponden a la variedad *salicinum*. En el caso de la variedad tipo, además de la novedad que supone su hallazgo en Valladolid, es la segunda vez que se refiere para Palencia (Fuertes *et al.* 1998). Por otra parte, en el caso de la variedad *salicinum* (tratada como *Brachythecium salicinum* Schimp. en Flora Briofítica Ibérica, Orgaz 2012), la localidad Burgalesa supone la primera cita provincial. Debido a las dificultades que entraña su identificación en ausencia de esporófito, es muy posible que esta variedad haya pasado desapercibida en otras partes del territorio.

***Bryum argenteum* Hedw.** – Madrid: 50. En un encinar, muy escaso.

***Ceratodon purpureus* (Hedw.) Brid.** – León: 42; Lugo: 48; Madrid: 51. Ocasional en robledales y encinares, siempre muy escaso.

***Cryphaea heteromalla* (Hedw.) D.Mohr** – Lugo: 48; Orense: 68. Presente sólo en robledales del noroeste del área de estudio. Muy escaso o escaso.

***Dialytrichia saxicola* (Lamy) M.J.Cano** – Cáceres*: 23. En un encinar, escaso.

***Dicranoweisia cirrata* (Hedw.) Lindb.** – Asturias: 2, 4; León: 47; Orense: 68; Salamanca: 81. Tan sólo en robledales del noroeste y el oeste del área de estudio. Muy escaso, salvo en la localidad 3, donde es moderadamente abundante.

***Dicranum scoparium* Hedw.** – Asturias: 1, 2, 3, 4; León: 46; Orense: 68. Restringido a los robledales del norte y noroeste del área de estudio. Muy escaso o escaso, salvo en la localidad 4, donde es moderadamente abundante (Fig. 5.1f).

***Didymodon insulanus* (De Not.) M.O.Hill** – Madrid: 67; Salamanca: 76; Toledo: 95. Ocasional en encinares de las zonas basales del territorio. Siempre muy escaso.

***Didymodon vinealis* (Brid.) R.H.Zander** – Burgos: 15; Cáceres: 17, 20; Toledo: 93. Ocasional en encinares de la cuenca del Tajo; también en un encinar del Norte de Burgos. Siempre muy escaso.

***Ditrichum heteromallum* (Hedw.) E.Britton** – Burgos*: 15. En un encinar, muy escaso.

***Fabronia pusilla* Raddi** – Cáceres: 17, 18, 19, 20, 21, 22, 23, 24, 26; Guadalajara: 38; León: 44; Madrid: 49, 50, 51, 52, 53, 54, 55, 56, 57, 58, 59, 67; Salamanca: 74, 77; Segovia*: 85; Toledo: 93**,** 94, 95, 96, 97. Restringido a encinares. Aparece principalmente en los tramos central y occidental de la cuenca del Tajo, donde resulta desde muy escaso hasta moderadamente abundante. También se encuentra en puntos dispersos de las mesetas Norte y Sur en los que es muy escaso, con la excepción de la localidad 74 (Arribes del Duero), en la que alcanza el nivel de moderadamente abundante (Fig. 5.1g).

***Grimmia laevigata* (Brid.) Brid.** – Ávila: 9; Madrid: 60; Segovia: 85. Ocasional en melojares y encinares del Sistema Central. Muy escaso o escaso.

***Grimmia lisae* De Not.** – Cáceres: 20, 21, 22, 23; Madrid: 52, 53, 54, 58; Salamanca*: 74, 75; Soria*: 89; Toledo: 93, 97, 99; Zamora*: 104, 105. Principalmente en encinares, sobre todo en los tramos central y occidental de la cuenca del Tajo, además ocasional en la meseta Norte. De muy escasa a escasa, según localidades. La localidad 99 (Robledo del Mazo) es excepcional por tratarse de un quejigar donde este musgo resulta moderadamente abundante (Fig. 5.1h).

Además de ser novedoso para las provincias de Salamanca y Soria, en Toledo sólo ha sido señalado en el reciente trabajo de Cezón & Muñoz (2013); las numerosas localidades que aportan estos autores junto con las indicadas en el presente catálogo muestran que este musgo es frecuente en la provincia sobre rocas y, en menor medida, sobre árboles.

***Grimmia pulvinata* (Hedw.) Sm.** – Ávila: 6; Burgos: 11, 14; Cáceres: 18**,** 20, 22, Cuenca, 27; Guadalajara: 37, 38; León: 42, 43, 44; Madrid: 49, 50, 52, 53, 54, 55, 56, 57**,** 59, 61, 64, 65, 66, 67; Palencia: 69, 71, 73; Salamanca: 76, 77, 78, 79; Segovia: 88; Toledo: 92, 93, 94**,** 95, 97, 99; Valladolid: 101, 102; Zamora: 103, 104, 105**,** 106, 107. Frecuente en encinares, ocasional en quejigares y excepcional en melojares, en ambas mesetas y a lo largo de la zona basal de la cuenca del

Tajo. Generalmente muy escaso y a veces escaso, pero al sur del Sistema Central alcanza, con cierta frecuencia, valores de moderadamente abundante (Fig. 5.2a).

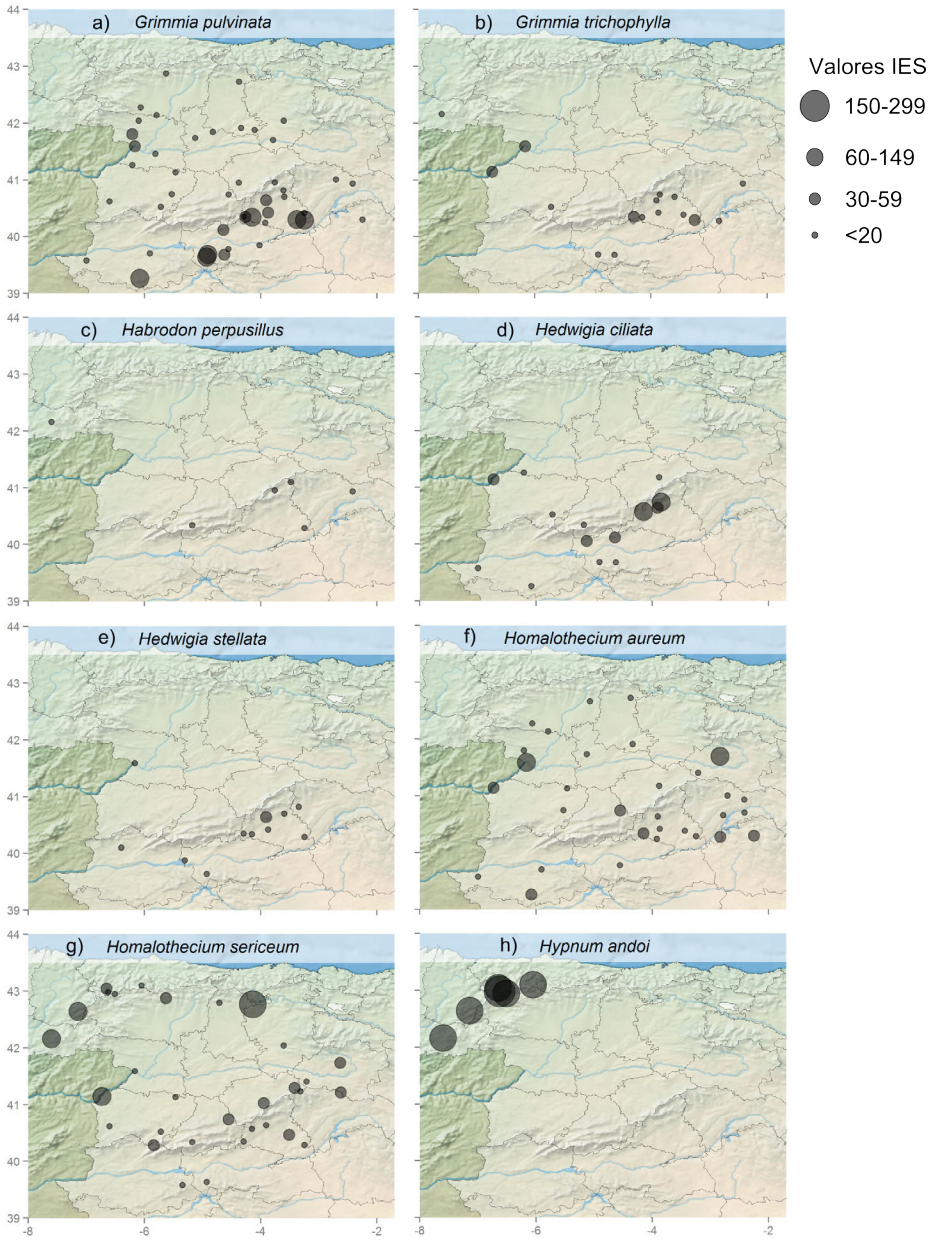

Figura 5.2: Mapas de distribución de algunas especies de briófitos epífitos recogidas en el catálogo. El tamaño de punto expresa la abundancia medida por medio del IES

***Grimmia trichophylla* Grev.** – Guadalajara: 35, 37; Madrid: 50, 51**,** 52, 53, 55, 57,

58, 59, 67; Orense: 68; Salamanca: 74**,** 77; Toledo: 94, 95; Zamora: 105. Frecuente en los encinares de la comunidad de Madrid y ocasional en los de otras áreas; raramente en quejigares o melojares. Muy escaso o escaso en todas las localidades del área de estudio (Fig. 5.2b).

***Habrodon perpusillus* (De Not.) LIndb.** – Ávila: 9; Guadalajara: 33, 37; Madrid: 55, 61; Orense: 68. Ocasional en bosques de cualquier tipo; aparece en localidades, normalmente en áreas montañosas, dispersas por el centro y noroeste peninsular. Siempre muy escaso (Fig. 5.2c).

***Hedwigia ciliata* (Hedw.) P.Beauv.** – Ávila: 9; Cáceres: 20, 22; Madrid: 50**,** 52, 58, 60; Salamanca: 74, 77; Segovia: 85; Toledo: 94, 95, 96**,** 97; Zamora: 104. Disperso en los encinares de del piedemonte del Sistema Central y de los Montes de Toledo, así como en los Arribes del Duero (loc. 74); raramente en melojares del Sistema Central. Muy escaso o escaso, aunque en bosques del sur de la Sierra de Guadarrama (locs. 58 y 60) llega a ser moderadamente abundante (Fig. 5.2d).

Todas las muestras analizadas corresponden a la variedad tipo.

***Hedwigia stellata* Hedenäs** – Cáceres: 17, 23; Guadalajara: 40; Madrid: 50**,** 52, 53, 55, 57, 59, 67; Toledo: 99; Zamora: 105. Presente en encinares y en un quejigar, en su mayoría del centro peninsular; también en algunos puntos de la cuenca occidental del Tajo; en la meseta Norte, tan sólo en la localidad zamorana de los Arribes del Duero (loc. 105). Muy escaso o, más raramente, escaso en el área de estudio (Fig. 5.2e).

En la provincia de Zamora es la segunda vez que se refiere este musgo (Casas *et al.* 1996).

***Homalothecium aureum* (Spruce) H.Rob.** – Ávila: 6; Burgos: 13; Cáceres: 18**,** 20, 22, Cuenca, 27; Guadalajara: 29, 35, 36, 37, 38; León: 42, 44, 45; Madrid: 51, 52, 53, 54, 55, 67; Palencia: 69, 71; Salamanca: 74, 76, 78; Segovia: 85; Soria: 89, 90; Toledo: 93; Valladolid: 102; Zamora: 105, 106. Principalmente en encinares aunque también en algunos quejigares y en un melojar. Frecuente en las dos mesetas, aunque especialmente en la Norte; ocasional en los tramos central y occidental de la cuenca del Tajo. Muy escaso o, más raramente, escaso; en las localidades 90 y 105 alcanza el nivel de moderadamente abundante (Fig. 5.2f).

Es la segunda vez que esta especie se cita para Valladolid y la localidad aquí referida es la tercera conocida en la provincia; en el caso de la de Zamora, las dos localidades que se aportan se suman a la única previamente conocida (Casas *et al.* 1985).

***Homalothecium lutescens* (Hedw.) H.Rob.** – León: 41; Palencia: 73; Salamanca: 81, 82; Soria: 90. Ocasional en todo tipo de bosques de la meseta Norte, donde es de muy escaso a escaso.

***Homalothecium sericeum* (Hedw.) Schimp.** –Asturias: 1, 2, 3, 4; Ávila: 6, 9; Burgos: 14, 16; Cáceres: 24, 25; Guadalajara: 34, 39; León: 43; Lugo: 48; Madrid: 52, 55, 59, 60, 64; Orense: 68; Palencia: 70, 72; Salamanca: 74, 76, 77, 79; Segovia: 83, 86; Soria: 89, 91; Toledo: 99; Zamora: 105. Común en bosques de las áreas montañosas del territorio, especialmente en robledales del Sistema Central y de la Cordillera Cantábrica; también en algunos quejigares orientales y en encinares dispersos, algunos en tierras bajas de ambas mesetas. Generalmente muy escaso o escaso, aunque frecuentemente con valores mínimos en encinares y algo mayores en melojares y quejigares. Alcanza niveles de moderadamente abundante en dos robledales del noroeste y en un encinar occidental y de abundante en la localidad 70, un quejigar norteño (Fig. 5.2g).

***Hypnum andoi* A.J.E.Sm.** – Asturias: 1, 2, 3, 4; Lugo: 48; Orense: 68. Común en los robledales de la Cordillera Cantábrica, donde es abundante o muy abundante (Fig. 5.2h).

***Hypnum cupressiforme* Hedw.** – Asturias: 1, 4; Ávila: 5, 6, 9; Burgos: 12, 13, 14, 15, 16; Cáceres: 19, 20, 22, 24, 25; Cuenca; 27; Guadalajara: 29, 31, 33, 35, 37, 38, 40; León: 42, 44; Lugo: 48; Madrid: 50, 52, 53, 58, 59, 60, 62, 63, 67; Orense: 68; Palencia: 69, 70, 71, 72, 73; Salamanca: 74, 76, 77, 79, 81; Segovia: 83, 84, 85, 86; Soria: 89, 90, 91; Toledo: 95, 98, 99; Zamora: 105, 106; Valladolid: 102. Ampliamente extendido en el territorio y especialmente abundante en diversas localidades periféricas. Muy escaso o escaso en la mayor parte de los puntos (Fig. 5.3a).

Aunque las muestras no se han podido identificar a nivel de variedad en todos los casos, sí se ha podido constatar la presencia de la variedad *cupressiforme* en Ávila (loc. 5), Burgos (locs. 14, 15, 16), Cuenca (loc. 27); Guadalajara (loc. 35, 38, 40), León (loc. 42), Madrid (loc. 58), Palencia (locs. 71, 73), Salamanca (locs. 74, 76, 77), Toledo (locs. 95, 99) y Zamora (locs. 105, 106). A su vez, la variedad *lacunosum* Brid. se encontró en Salamanca (loc. 74) y Soria (locs. 89, 90). Por último, se ha constatado la presencia de la variedad *resupinatum* (Taylor) Schimp. en Asturias (locs. 1, 4), Ávila (loc. 6), Burgos (locs.13, 14, 15, 16), Cáceres (locs. 20, 22, 24, 25), Cuenca (locs. 27), Guadalajara (locs. 29, 31, 35, 37, 38, 40), León (locs. 42, 44), Madrid (locs. 50, 58), Orense (loc. 68), Palencia (locs. 69, 70, 72,

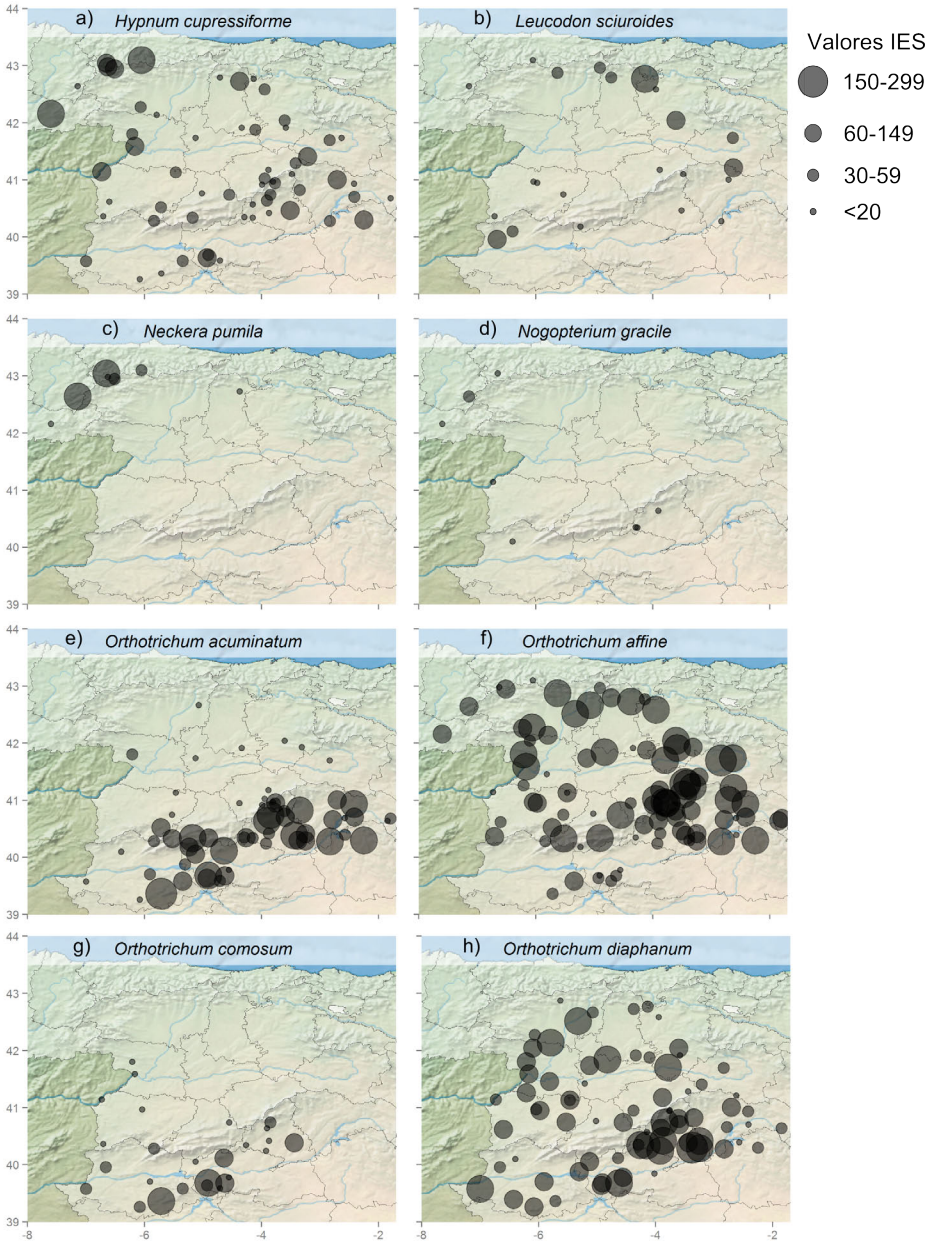

Figura 5.3: Mapas de distribución de algunas especies de briófitos epífitos recogidas en el catálogo. El tamaño de punto expresa la abundancia medida por medio del IES

73), Salamanca (locs. 76, 79, 81), Segovia (loc. 85), Soria (locs. 89, 90, 91), Toledo (locs. 95, 98, 99), Valladolid (loc. 102). En el caso de la variedad *cupressiforme*, además de la novedad que supone la localidad de Soria, en Salamanca se había

señalado una sola vez (Rupidera & Elías 1994). En cuanto a la var. *lacunosum*, es la segunda vez que se refiere en Salamanca (Rupidera & Elías 1994) y Soria. Finalmente, la variedad *resupinatum* representa una novedad para las provincias de Burgos, Cuenca, Guadalajara, Soria, Toledo y Valladolid, y es la segunda vez que se refiere para Ávila (Albertos *et al.* 1997), Cáceres (Elías *et al.* 2006) y Salamanca (Rupidera & Elías 1994).

***Hypnum vaucheri* Lesq.** – Cáceres*: 22. En un encinar, muy escaso.

La recolección ha constituido la primera localidad conocida para la provincia (Ríos & Medina, 2014 como *Hypnum cupressiforme* var. *julaceum*) y supone una de las cuatro constatadas en España hasta la fecha (Brugués, Ruíz & Cros 2014).

***Isothecium alopecuroides* (Lam. *ex* Dubois) Isov.** – Asturias: 3. En un robledal, moderadamente abundante.

***Isothecium myosuroides* Brid.** – Asturias: 3, 4; Lugo: 48; Orense: 68. Restringida a los robledales del extremo noroeste, donde resulta de muy escaso a moderadamente abundante.

***Leptodon smithii* (Hedw.) F. Weber & D. Mohr** – Salamanca: 74. En un encinar, muy escaso.

***Leucodon sciuroides* (Hedw.) Schwägr.** – Asturias: 1; Ávila: 8; Burgos: 13**,** 14, 15, 16; Cáceres: 21, 23, 26; Guadalajara: 33, 35**,** 38, 39; León: 43, 45, 46; Lugo: 48; Palencia: 70, 72; Salamanca: 78**,** 80, 81, 82; Segovia: 85; Soria: 91. En bosques de las áreas montañosas y del piedemonte en el centro, oriente y norte del territorio y en algunas localidades basales de la meseta Norte; más frecuente en encinares y quejigares que en melojares. Comúnmente muy escaso o escaso, alcanza niveles de medianamente abundante en algunos encinares y quejigares, y de abundante en la localidad 70, en uno de estos últimos bosques (Fig. 5.3b).

Se ha constatado la presencia de la variedad *morensis* en las provincias de Guadalajara (loc. 39), León (loc. 43) y Palencia (locs. 70, 72) localidades en las que también se encontró la variedad tipo.

***Neckera pumila* Hedw.** – Asturias: 1, 2, 3, 4; Lugo: 48; Orense: 68; Palencia*: 69. Restringido a la Cordillera Cantábrica, generalmente en robledales pero también en un encinar. Muy escaso o escaso, abundante tan sólo en las localidades 3 y 4 (Fig. 5.3c).

***Nogopterium gracile* (Hedw.) Crosby & W.R.Buck** – Asturias: 3; Cáceres: 23; Lugo: 48; Madrid: 52, 56, 59; Orense: 68; Salamanca: 74. Disperso, en melojares de las montañas noroccidentales y en encinares de la parte basal del Sistema Central y de los Arribes del Duero. Escaso en un robledal (loc. 48), en el resto muy escaso (Fig. 5.3d).

***Nyholmiella obtusifolia* (Brid.) Holmen & Warncke** – Madrid: 60; Segovia: 83, 84. Hallado tan sólo en tres melojares de la Sierra de Guadarrama, donde es muy escaso.

***Orthotrichum acuminatum* H.Philib.** – Ávila: 7, 8, 9, 10; Burgos*: 13, 14; Cáceres: 17, 18, 19, 20, 22, 23, 24, 25, Cuenca**,** 27; Guadalajara: 28, 29, 30, 31, 32, 35, 36**,** 37, 38, 40; León*: 45; Madrid: 49, 50, 51, 52, 53**,** 54, 55, 56, 57, 58, 59, 61, 62, 63**,** 64, 65, 66, 67; Palencia*: 71; Salamanca: 75, 77, 78; Segovia: 83, 84, 85, 88; Soria: 90; Toledo: 93, 94, 95, 96**,** 97, 98, 99; Valladolid*: 102; Zamora*: 106. Muy común en encinares, especialmente de la cuenca del Tajo, donde también se encuentra en algunos quejigares; frecuente igualmente en los melojares del Sistema Central. Al sur de esta cordillera es a menudo moderadamente abundante o abundante y en la localidad 19 alcanza el nivel máximo de muy abundante; al norte es muy escaso o, excepcionalmente, escaso (Fig. 5.3e).

Este musgo era desconocido en la mayor parte de la meseta Norte. Además, en Soria sólo se conocía de una localidad (Medina, 2006; Medina *et al.*, 2010) y para Salamanca es la segunda vez que se refiere, aunque se conocían dos localidades (Mateo, Zafra & Varo 1990).

***Orthotrichum affine* Schrad. ex Brid.** – Asturias: 1, 2, 4; Ávila: 5, 6, 7, 8, 10; Burgos: 11, 12, 13, 14, 15, 16; Cáceres: 19, 24, 25, Cuenca, 27; Guadalajara: 28, 29, 30, 31, 32, 33, 34, 35, 36, 37, 38, 39, 40; León: 41, 42, 43, 44, 45, 46, 47; Lugo: 48; Madrid: 49, 50, 51, 52, 53, 54, 55, 57, 58, 59, 60, 61, 62, 63, 64, 65, 66; Orense: 68; Palencia: 69, 70, 71, 72, 73; Salamanca: 74, 75, 76, 77, 78, 79, 80, 81, 82; Segovia: 83, 84, 85, 86, 87, 88; Soria: 89, 90, 91; Toledo: 93, 94, 95, 98, 99; Valladolid*: 101, 102; Zamora: 103, 104, 105, 106, 107. Común en todo tipo de bosques y en casi toda el área de estudio; ausente tan sólo de algunas localidades dispersas, en su mayor parte de los tramos central y occidental de la cuenca del Tajo. Moderadamente abundante o abundante en muchos de los bosques montanos, ocasionalmente muy abundante (locs. 87 y 90); muy escaso o escaso en distintas localidades, muchas de ellas correspondientes a la zona central de las mesetas Norte y Sur (Fig. 5.3f).

Previamente desconocido en Valladolid, en Palencia había sido señalado en una sola localidad (Fuertes *et al.* 1998).

Orthotrichum anomalum **Hedw.** – Guadalajara: 35. En un encinar, muy escaso.

Orthotrichum columbicum **Mitt.** – Asturias: 2, 4. Ocasional en robledales del noroeste. Escaso y moderadamente abundante.

Orthotrichum comosum **F.Lara, R.Medina & Garilleti** – Ávila*: 6; Cáceres: 18**,** 19, 20, 22, 24, 25, 26; Madrid: 51, 52, 53**,** 54, 56, 58; Salamanca*: 74, 81, 82; Toledo: 93, 94, 95**,** 96, 97, 98, 99; Valladolid*: 101; Zamora*: 105, 106. Frecuente en los encinares y ocasional en melojares y quejigares de los tramos central y occidental de la cuenca del Tajo; en la meseta Norte solo en algunos encinares, casi todos del sector más occidental del área de estudio. Muy escaso en las localidades al norte del Sistema Central y en algunos puntos de en los tramos central y occidental de la cuenca del Tajo; en esta última área frecuentemente resulta escaso, pero llega a alcanzar niveles de moderadamente abundante y abundante en los encinares de las localidades 19 y 95 (Fig. 5.3g).

Desconocido en las provincias de Castilla y León; para Madrid, Toledo y Cáceres se conocían solo dos localidades por provincia (R. Medina *et al.* 2013; Lara & Garilleti 2014), algunas de las cuales son fruto del presente estudio.

Orthotrichum cupulatum **Hoffm. ex Brid.** – Burgos: 14. En un encinar, muy escaso.

La muestra corresponde a la variedad tipo.

Orthotrichum diaphanum **Schrad. ex Brid.** – Ávila: 5, 6; Burgos: 11, 12, 14, 15; Cáceres: 17, 18, 19, 20, 21, 22, 23, 26, Cuenca, 27; Guadalajara: 29, 30, 32, 35, 36, 37, 38, 39, 40; León: 41, 42, 43, 44, 45; Madrid: 49, 50, 51, 52, 53, 54, 55, 56, 57, 58, 59, 60, 61, 63, 64, 65, 66, 67; Palencia: 69, 70, 71, 73; Salamanca: 74, 75, 76, 78, 79, 80, 82; Segovia: 85, 87, 88; Soria: 89, 90; Toledo: 92, 93, 94, 95, 96, 97, 99; Valladolid*: 100, 101, 102; Zamora: 103, 104, 105, 106, 107. Muy frecuente en los encinares y quejigares de las mesetas Norte y Sur y en los tramos central y occidental de la cuenca del Tajo; ocasionalmente en melojares. Con abundancias muy variables, resulta muchas veces moderadamente abundante o abundante y alcanza el nivel de muy abundante en la localidad 49 (Fig. 5.3h).

Desconocido previamente en Valladolid; para Palencia solo se había citado una localidad (Fuertes & Mendiola 1986).

***Orthotrichum ibericum* F.Lara & Mazimpaka** – Ávila: 7, 10; Cáceres: 24, 25; Toledo: 95. En melojares del sector centro-occidental del Sistema Central y de los Montes de Toledo, donde casi siempre resulta moderadamente abundante.

***Orthotrichum lyellii* Hook. & Taylor** – Asturias: 1, 2, 3, 4; Ávila: 6, 7, 8, 9, 10; Burgos: 12, 13, 14, 15, 16; Cáceres: 17, 18, 19, 20, 22, 23, 24, 25, 26, Cuenca, 27; Guadalajara: 28, 33, 34, 35, 36, 37, 38, 39; León: 41, 42, 43, 44, 45, 46, 47; Lugo: 48; Madrid: 49, 50, 51, 52, 53, 54, 55, 56, 57, 58, 59, 60, 61, 62, 63, 64, 65, 67; Orense: 68; Palencia: 69, 72, 73; Salamanca: 74, 76, 77, 78, 79, 80, 81, 82; Segovia: 83, 84, 85, 86, 87, 88; Soria: 89, 90, 91; Toledo: 93, 94, 95, 96, 97, 98, 99; Valladolid*: 102; Zamora: 105, 106, 107. Frecuente en todo tipo de bosques, sobre todo en encinares y melojares de las zonas montanas del área de estudio. Muy variable en abundancia, en las localidades del Sistema Central, del Sistema Ibérico Norte y de la Cordillera Cantábrica es con frecuencia moderadamente abundante o abundante y, en esta última zona, llega a alcanzar el nivel de muy abundante (loc. 72); en los encinares y quejigares de las dos mesetas es normalmente muy escaso o escaso (Fig. 5.4a).

Desconocido previamente en Valladolid; para la provincia de Palencia solo había sido citado por Fuertes & Mendiola ((1986), que proporcionaron dos localidades.

***Orthotrichum macrocephalum* F.Lara, Garilleti & Mazimpaka** – Cáceres*: 18; Guadalajara: 35; Madrid: 52, 58, 60, 66; Toledo*: 94, 95. En encinares, raramente melojares y quejigares, de la cuenca del Tajo, fundamentalmente en los piedemontes de los sistemas montañosos. Muy escaso o escaso (Fig. 5.4b).

***Orthotrichum pallens* Bruch ex Brid.** – Cuenca, 27; Guadalajara: 29, 30; Madrid*: 55**,** 66; Soria*: 90. Tan sólo en encinares y quejigares de la parte oriental del área de estudio. Muy escaso o escaso.

Novedad para Madrid y Soria, la localidad de Cuenca supone además la segunda cita para la provincia (Puche *et al.* 2006).

***Orthotrichum philibertii* Venturi** – Ávila*: 6; Cáceres: 17, 18, 20**,** 21, 22; León*: 43; Madrid*: 53, 56; Salamanca*: 74, 80; Toledo: 94, 95**,** 96, 97; Valladolid*: 102; Zamora*: 103, 104. Relativamente frecuente en encinares de los tramos central y occidental de la cuenca del Tajo, más raro en los de la meseta Norte, donde también se ha encontrado en un quejigar. Generalmente muy escaso, a veces escaso y, en la localidad 74 de los Arribes del Duero, moderadamente abundante (Fig. 5.4c).

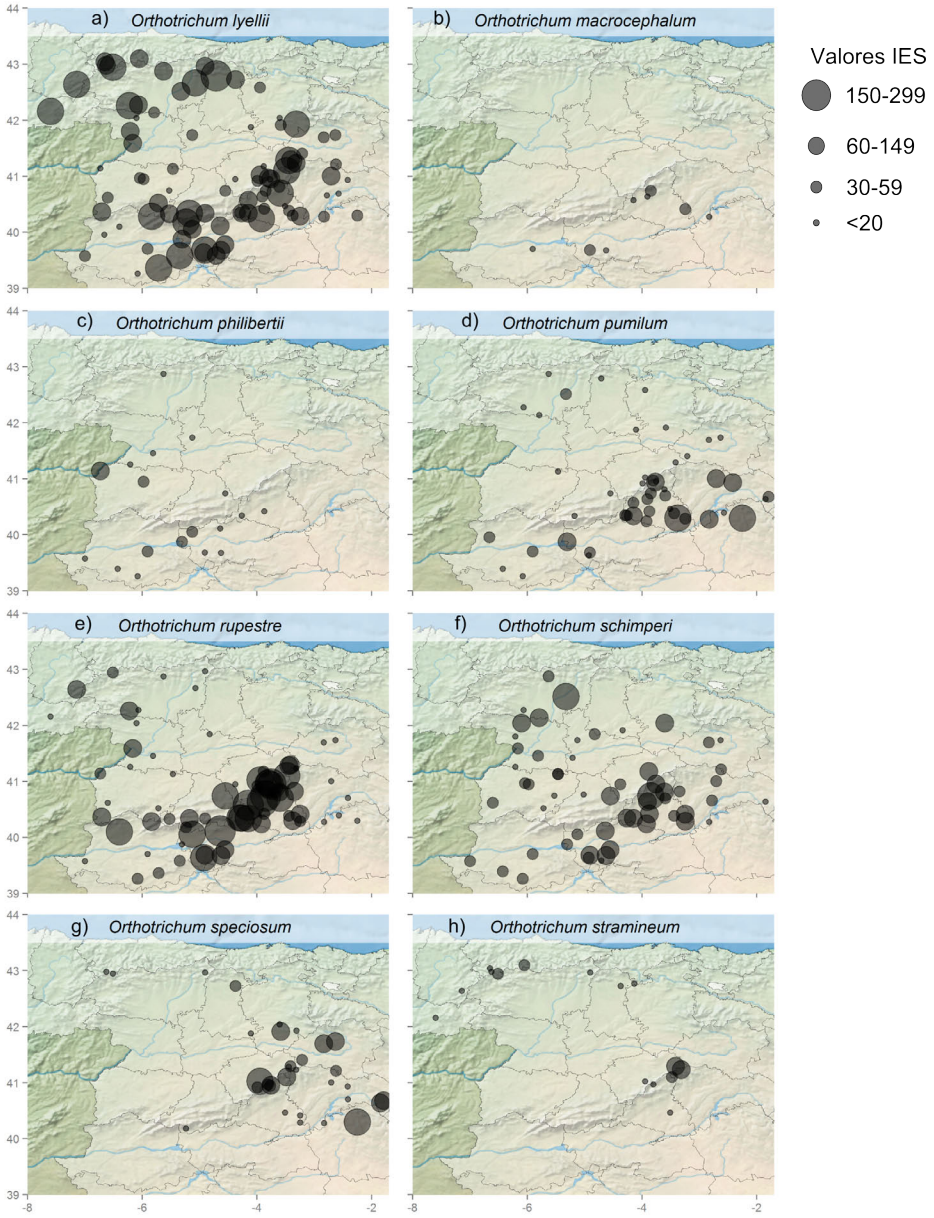

Figura 5.4: Mapas de distribución de algunas especies de briófitos epífitos recogidas en el catálogo. El tamaño de punto expresa la abundancia medida por medio del IES

Este musgo era desconocido al norte del Sistema Central. Además de tratarse de una novedad para 5 provincias, supone la segunda referencia para Cáceres (Mazimpaka, Lara & Garilleti 1999) y Toledo (Cezón & Muñoz 2013), aunque para esta última provincia se dieron a conocer una decena de localidades.

***Orthotrichum pumilum* Sw. ex anon.** – Ávila: 6, 9; Burgos*: 12, 15, 16; Cáceres*: 17, 18, 20, 21, 26, Cuenca, 27; Guadalajara: 28, 30, 31, 32, 35, 37, 38; León*: 41, 42**,** 43, 44; Madrid: 49, 50, 51, 52, 53, 54, 55**,** 56, 57, 58, 59, 60, 61, 62, 63, 64**,** 65, 67; Palencia*: 72, 73; Salamanca: 76; Segovia: 83, 84, 86; Soria: 89**,** 90, 91; Toledo: 95, 99. En todo tipo de bosques pero más frecuente en encinares; repartido por gran parte del territorio aunque especialmente común hacia el este y el sur y muy raro hacia el extremo oeste. Muy escaso y excepcionalmente escaso en las localidades de la meseta Norte; de muy escaso a moderadamente abundante en los bosques del Sistema Central y más al sur; abundante en solo un par de encinares (locs. 27 y 49) del centro-este peninsular (Fig. 5.4d).

Además de ser novedoso en cuatro provincias, supone la segunda referencia para Salamanca (Luisier 1924) y Toledo (Cezón & Muñoz 2013), aunque para esta última provincia se publicaron varias localidades. Para Ávila y Segovia existen citas previas, aunque no se ha podido comprobar que realmente correspondan a esta especie y no a *O. schimperi* (Lara & Garilleti 2014).

***Orthotrichum rupestre* Schleich. ex Schwägr.** – Asturias: 4; Ávila: 6, 7, 8, 9, 10; Burgos: 13; Cáceres: 17, 18, 19, 20, 22, 23, 24, 25, Cuenca, 27; Guadalajara: 29, 32, 33, 34, 35, 38, 40; León: 42, 43, 45, 46, 47; Lugo: 48; Madrid: 49, 50, 51, 52, 53, 54, 55, 56, 57, 58, 59, 60, 61, 62, 63, 64, 65, 66, 67; Orense: 68; Salamanca: 74, 76, 77, 79, 81; Segovia: 83, 84, 85, 86, 87, 88; Soria: 90, 91; Toledo: 93, 94, 95, 96, 97, 98, 99; Valladolid*: 101; Zamora: 103, 104, 105, 107. Muy común en los bosques de todo el territorio. Muestra todos los niveles de abundancia posibles en las distintas localidades. Es abundante en melojares del Sistema Central y en encinares y quejigares meridionales y llega a ser muy abundante en un melojar guadarrámico y en varios encinares de Madrid y Toledo (Fig. 5.4e).

***Orthotrichum schimperi* Hammar** – Ávila: 5, 6; Burgos: 14; Cáceres*: 17, 18**,** 20, 21, 22; Guadalajara: 30, 35, 36, 38, 39, 40; León: 41, 42, 43, 44; Madrid: 50, 51, 52, 53, 54**,** 55, 56, 57, 58, 61, 65, 66, 67; Palencia*: 71; Salamanca: 75, 76, 77, 78, 79, 80, 82; Segovia: 85, 88; Soria: 90, 91; Toledo: 93, 94, 95, 96, 97, 98, 99; Valladolid*: 100, 101, 102; Zamora: 103, 104, 105, 106, 107. Muy común en los encinares de todo el territorio; también en algunos quejigares, pero es muy raro en melojares. De muy escaso a abundante según las localidades, los bosques con mayor representación de esta especie son encinares y quejigares concentrados en Madrid y Toledo y encinares dispersos por el este, norte y noroeste de la meseta Norte (Fig. 4f).

Se ha encontrado por segunda vez en las provincias de Ávila, Salamanca y Zamora (Lara & Garilleti 2014), así como en la de Burgos (Heras *et al.* 2014). Además, para Toledo se ha citado sólo recientemente (Cezón & Muñoz 2013), aunque se indicaron varias localidades.

***Orthotrichum speciosum* Nees** – Asturias: 2, 4; Ávila: 8; Burgos: 12, 13, 14, 16; Cuenca: 27; Guadalajara: 29, 30, 31, 33, 34, 35, 37, 38, 39; León: 46; Madrid: 55, 61, 62, 63, 64, 66; Palencia*: 69, 73; Segovia: 83, 84, 86, 87; Soria: 89, 90, 91. Frecuente en todo tipo de bosques de las zonas altas del extremo oriental del territorio y ocasional en la Cordillera Cantábrica. De muy escaso a abundante, los valores más altos se alcanzan en encinares, melojares y, en menor medida, quejigares del Sistema Ibérico y del sector oriental del Sistema Central (Fig. 5.4g).

Todos los especímenes estudiados corresponden a la variedad típica. Además de ser novedad para Palencia, la localidad que se aporta para la provincia de Ávila se suma a las dos incluidas en la única referencia previa (Elías *et al.* 2006).

***Orthotrichum stramineum* Hornsch. *ex* Brid.** – Asturias: 1, 2, 3, 4; Burgos: 16; Guadalajara: 33, 34; León: 46; Lugo: 48; Madrid: 62, 64; Orense: 68; Palencia*: 69, 70; Segovia: 83, 86. En melojares y algunos quejigares, más raramente en encinares, de la cordillera Cantábrica y del oriente del Sistema Central; extraordinario en la meseta Sur. Muy escaso en la mayoría de las localidades; a veces escaso en localidades del norte y moderadamente abundante en la sierra de Ayllón (Fig. 5.4h).

***Orthotrichum striatum* Hedw.** – Asturias: 1, 2, 3, 4; Ávila: 6, 7, 8, 9, 10; Burgos: 12, 13, 14, 16; Cáceres: 24, 25, Cuenca, 27; Guadalajara: 29, 31, 32, 33, 34, 35, 37, 38, 39, 40; León: 41, 42, 43, 45, 46, 47; Lugo: 48; Madrid: 51, 52, 53, 55, 57, 58, 60, 61, 62, 63, 64, 65; Orense: 68; Palencia: 69, 70, 72, 73; Salamanca: 77, 81; Segovia: 83, 84, 85, 86, 87, 88; Soria: 89, 90, 91; Toledo: 94, 95, 96, 98, 99; Valladolid*: 101; Zamora: 106, 107. Muy común en robledales de todo el territorio y esporádico en encinares y quejigares de ambas mesetas. Desde muy escaso hasta abundante, los valores más altos se alcanzan de forma general en melojares, especialmente en el Sistema Central y los Montes de Toledo (Fig. 5.5a).

Además de ser novedad para Valladolid, las localidades palentinas confirman la presencia de la especie en la provincia (Fuertes & Mendiola 1986).

***Orthotrichum tenellum* Bruch ex Brid.** – Ávila: 6, 9, 10; Burgos: 12, 14; Cáceres: 17, 18, 19, 20, 21, 22, 23, 24, 25, 26; Guadalajara: 29, 32, 33, 35, 38, 39, 40; León: 41, 42, 43, 44, 45; Madrid: 49, 50, 51, 52, 53, 54, 55, 56, 57, 58, 59, 60, 61, 64,

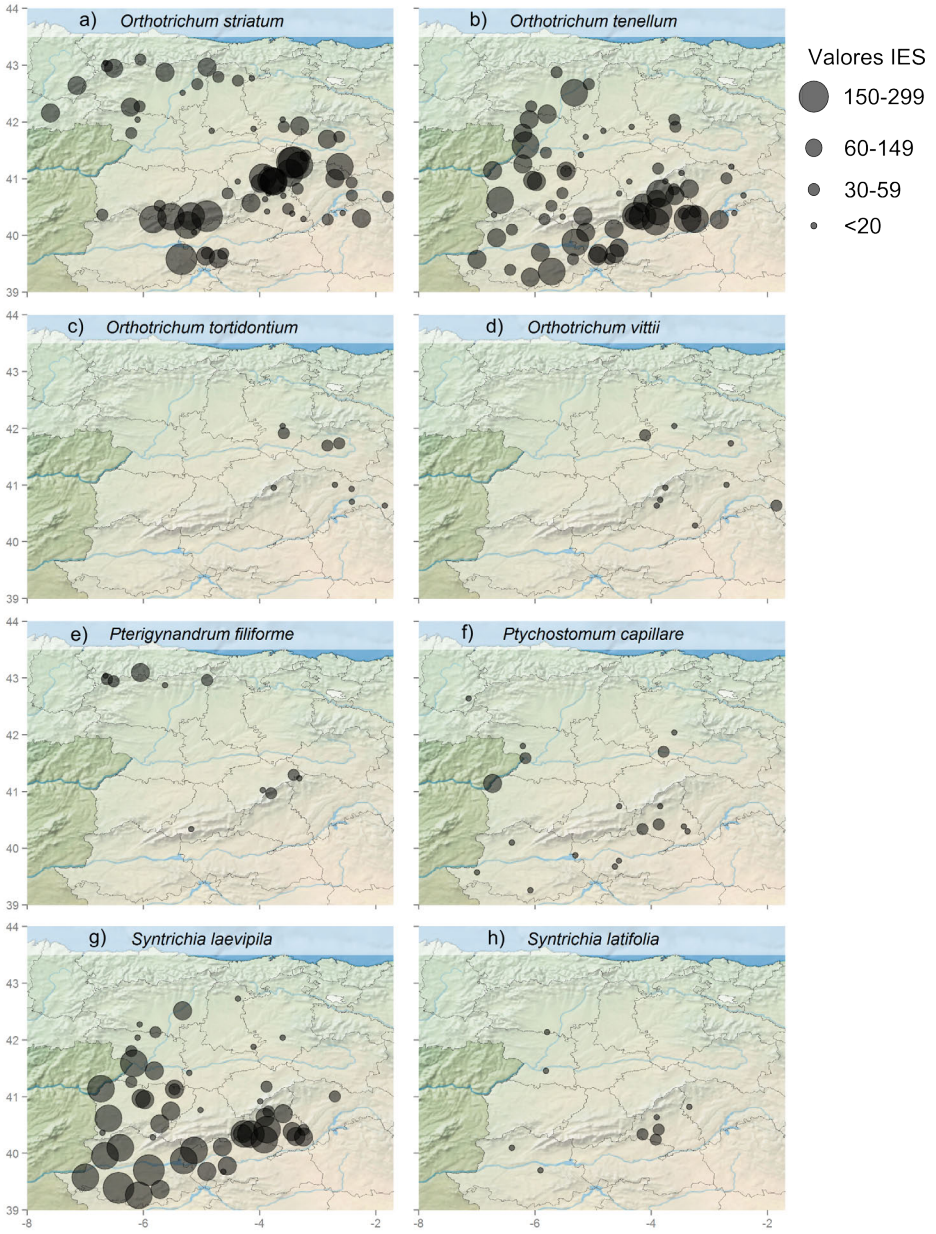

Figura 5.5: Mapas de distribución de algunas especies de briófitos epífitos recogidas en el catálogo. El tamaño de punto expresa la abundancia medida por medio del IES

65, 66, 67; Orense: 68; Palencia*: 71; Salamanca: 74, 75**,** 76, 77, 78, 79, 80, 81, 82; Segovia: 85, 88; Toledo: 93, 94, 95, 96, 97, 98, 99; Valladolid*: 100**,** 101, 102; Zamora: 103, 104, 105, 106, 107. Muy común en encinares del territorio, aunque en la meseta Norte solo es frecuente en tierras bajas; resulta además esporádico en

quejigares y melojares; prácticamente ausente en la Cordillera Cantábrica. De muy escaso a abundante, muestra muy frecuentemente valores altos en los bosques, casi siempre encinares, de las zonas bajas de la cuenca del Tajo y del oeste de la cuenca del Duero (Fig. 5.5b).

Novedad para Palencia y Valladolid, en Segovia es la segunda vez que se cita (Lara, Mazimpaka & Garilleti 1997).

***Orthotrichum tortidontium* F.Lara, Garilleti & Mazimpaka** – Burgos: 12, 14; Guadalajara: 29, 30, 37, 38; Madrid: 61; Soria: 90, 91. Únicamente en quejigares y encinares de zonas montanas del oriente del territorio. Muy escaso o escaso (Fig. 5.5c).

Previamente sólo se conocían sendas localidades en Burgos y en Madrid para esta especie (Lara, Garilleti & Mazimpaka 1996).

***Orthotrichum vittii* F.Lara, Garilleti & Mazimpaka** – Burgos: 14; Guadalajara: 30, 38; Madrid: 52, 55, 58, 61; Palencia*: 73; Soria: 91. Tan sólo en encinares y quejigares del extremo oriental del área de estudio. Muy escaso o, en un par de quejigares, escaso (Fig. 5.5d).

La cita de Burgos es la segunda para la provincia (Lara *et al.* 1999).

***Pterigynandrum filiforme* Hedw.** – Asturias: 1, 2, 3, 4; Ávila: 9; Guadalajara: 34; León: 43, 46; Madrid: 62; Segovia: 83, 86. En robledales y algún encinar de la Cordillera Cantábrica, así como en melojares del Sistema Central. Muy escaso o escaso, de manera extraordinaria abundante en la localidad 1 (Fig. 5.5e).

***Ptychostomum capillare* (Hedw.) Holyoak & N. Pedersen** – Ávila: 6; Burgos: 11, 14; Cáceres: 17, 20, 22, 23; Lugo: 48; Madrid: 49, 51**,** 53, 58, 67; Salamanca: 74; Toledo: 93, 94; Zamora: 105, 106. Esporádico en encinares de la meseta norte y de los tramos central y occidental de la cuenca del Tajo; también en un robledal noroccidental. Generalmente muy escaso, en ocasiones escaso y moderadamente abundante solo en la localidad 74 de los Arribes del Duero (Fig. 5.5f).

***Syntrichia calcicola* J.J.Amann** - Valladolid*: 102. En un quejigar, muy escaso.

***Syntrichia laevipila* Brid.** – Ávila: 5; Burgos: 14; Cáceres: 17, 18, 19, 20, 21, 22, 23, 25, 26; Guadalajara: 38; León: 41, 42, 44; Madrid: 49, 50, 51, 52, 53, 54, 55, 56, 57, 58, 59, 66, 67; Palencia: 69, 73; Salamanca: 74, 75, 76, 77, 78, 79, 80, 81, 82; Segovia: 84, 85; Toledo: 93, 94, 95, 96, 97; Valladolid*: 100**,** 102; Zamora: 103, 104, 105, 106, 107. Muy común, sobre todo en el sur y oeste del territorio,

casi siempre en encinares. Muestra todos los niveles de abundancia en las distintas localidades; con gran frecuencia moderadamente abundante o abundante en la meseta Sur y en las zonas bajas de todo el sector occidental, alcanza a ser muy abundante en las localidades 18 y 21 del extremo suroeste del territorio (Fig. 5.5g).

Novedad para Valladolid y segunda vez que se cita para la provincia de Palencia (Fuertes & Mendiola 1986).

***Syntrichia latifolia* (Bruch ex Hartm.) Huebener** – Cáceres*: 18, 23; Guadalajara*: 40; León: 44; Madrid: 52, 53, 54, 67; Zamora: 103. Ocasional en encinares, sobre todo en el tramo central de la cuenca del Tajo. Muy escaso o escaso (Fig. 5.5h).

Novedad para Cáceres y Guadalajara, se aporta además la segunda localidad para Zamora (Luisier 1924).

***Syntrichia minor* (Bizot) M.T.Gallego, J.Guerra, M.J.Cano, Ros & Sánchez-Moya** – Toledo: 92, 93. Ocasional en encinares, donde resulta muy escaso.

Se aporta la segunda localidad para la provincia de Toledo (Cezón & Muñoz 2013).

***Syntrichia papillosa* (Wilson) Jur.** – Cáceres*: 17, 18, 19**,** 20, 21, 22, 23, Cuenca, 27; Guadalajara: 35, 38, 40; León*: 41, 44; Madrid: 49, 50, 51, 52, 53, 54**,** 55, 56, 57, 58, 59, 60, 65, 67; Palencia*: 72; Salamanca: 76, 79, 82; Toledo: 92, 93, 94, 95, 96, 97; Zamora: 105. Común en encinares de la cuenca del Tajo y, en menor medida, del centro y oeste de la cuenca del Duero; raramente en quejigares o melojares. Normalmente muy escaso o escaso, llega a ser abundante en diversos encinares de Madrid (Fig. 5.6a).

Es novedad para Cáceres, León y Palencia y se cita por segunda vez para Salamanca (Elías *et al.* 1994), Toledo (Cezón & Muñoz 2013) y Zamora (Albertos *et al.* 2005), aunque en todas ellas se conocía más de una localidad.

***Syntrichia papillosissima* (Copp.) Loeske** – Madrid*: 55; Soria: 89, 90; Valladolid: 101. Esporádico en encinares de ambas mesetas, todos en la mitad oriental del territorio. Muy escaso siempre.

Novedad para Madrid y segunda cita para la provincia de Valladolid (Casas & Brugués (1974), donde se conocían dos localidades.

***Syntrichia princeps* (De Not.) Mitt.** – Ávila: 6; Burgos: 15; Cáceres: 18, 19, 20, 21, 22, 26; León*: 44; Madrid: 58, 60, 66; Palencia: 71; Salamanca: 74, 76, 78**,** 79, 80; Soria*: 89; Toledo: 93, 94, 95, 97; Valladolid*: 101, 102; Zamora: 105. Frecuente en bosques, casi siempre encinares, tanto en la meseta Norte como en

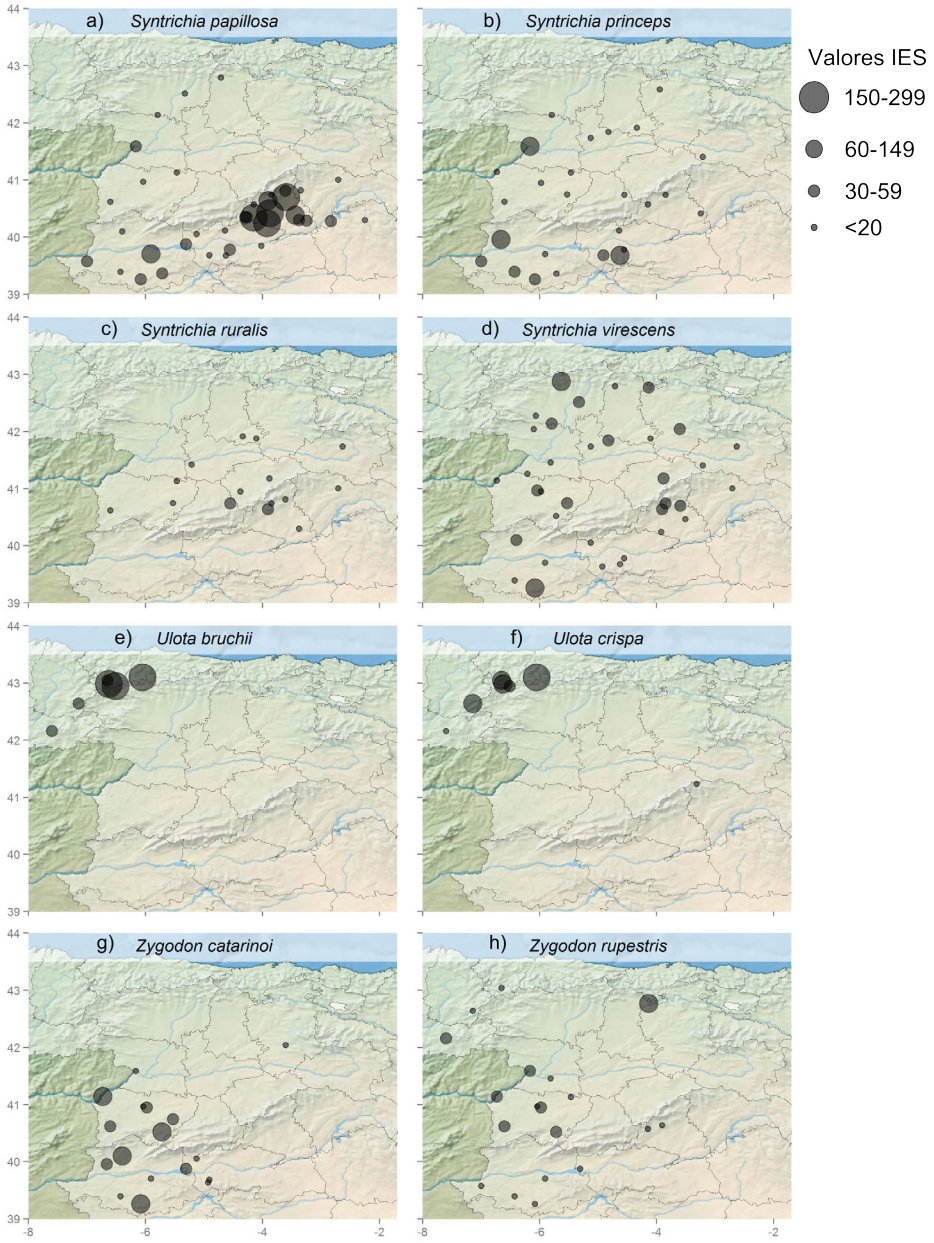

Figura 5.6: Mapas de distribución de algunas especies de briófitos epífitos recogidas en el catálogo. El tamaño de punto expresa la abundancia medida por medio del IES

los tramos central y occidental de la cuenca del Tajo. Generalmente muy escaso; escaso en algunos encinares de la cuenca del Tajo y moderadamente abundante en otros encinares de la misma área y de las tierras bajas zamoranas (Fig. 5.6b).

Novedad para León, Soria y Valladolid, previamente solo existían sendas citas para Burgos (Allorge 1930) y Palencia (Casas 1952).

***Syntrichia ruralis* (Hedw.) F.Weber & D.Mohr** – Ávila: 6; Burgos: 14; Guadalajara: 38; Madrid: 49, 52, 58, 65; Palencia: 71, 73; Salamanca: 76, 78, 79; Segovia: 85, 88; Soria: 91; Valladolid: 100. En encinares y algunos quejigares de la meseta Norte y del sector oriental de la meseta Sur. Muy escaso o, en algunas localidades próximas al Sistema Central, escaso (Fig. 5.6c).

Todos los especímenes estudiados corresponden a la variedad típica.

***Syntrichia subpapillosissima* (Bizot & R.B.Pierrot ex W.A.Kramer) M.T.Gallego & J.Guerra** – Ávila: 6. En un encinar, escaso.

***Syntrichia virescens* (De Not.) Ochyra** – Burgos*: 14, 16; Cáceres*: 18**,** 20, 21, 23; Guadalajara: 38; León: 41, 42, 43, 44; Madrid: 50**,** 52, 54, 57, 58; Palencia*: 70, 72, 73; Salamanca: 74**,** 77, 78, 80, 82; Segovia: 85; Soria: 89, 91; Toledo: 93, 94**,** 96, 99; Valladolid*: 101, 102; Zamora: 103, 104, 107. Frecuente en encinares de la meseta Norte y, en menor medida, en los tramos central y occidental de la cuenca del Tajo; también en quejigares dispersos y algún melojar de la misma área. Muy escaso o escaso, llega a ser moderadamente abundante en un par de encinares (locs. 20 y 43) situados en los extremos de cada una de las mesetas (Fig. 5.6d).

Además de la novedad que supone para cuatro provincias, en las de León y Zamora se había citado una única vez (Albertos *et al.* 2005).

***Tortella humilis* (Hedw.) Jenn.** – Burgos: 15; Guadalajara: 35, 38. Ocasional en encinares del oriente del área de estudio. Muy escaso o escaso.

***Tortella inclinata* (R.Hedw.) Limpr.** – Palencia: 69. En un encinar, escaso.

Es la segunda vez que se refiere para la provincia de Palencia (Geissler 1979).

***Tortella inflexa* (Bruch) Broth.** – Guadalajara*: 35. En un encinar, muy escaso.

***Tortula muralis* Hedw.** – Salamanca: 74; Toledo: 93. Ocasional en encinares. Muy escaso.

***Tortula subulata* Hedw.** – Ávila: 6; Burgos: 11; Salamanca: 76. Ocasional en encinares de la cuenca del Duero. Siempre muy escaso.

***Ulota bruchii* Hornsch. ex Brid.** – Asturias: 1, 2, 3, 4; Lugo: 48; Orense: 68. Restringido a los robledales noroccidentales. Escaso o abundante según las localidades (Fig. 5.6e).

***Ulota coarctata* (P.Beauv.) Hammar** – Asturias: 1, 2, 3, 4. En algunos robledales noroccidentales. Muy escaso o escaso.

***Ulota crispa* (Hedw.) Brid.** – Asturias: 1, 2, 3, 4; Guadalajara: 34; Lugo: 48; Madrid: 64; Orense: 68. Restringido a los robledales noroccidentales. Generalmente de muy escaso a moderadamente abundante; abundante sólo en la localidad 1 (Fig. 5.6f).

Ulota crispula Bruch – Asturias: 1, 2, 3, 4; Lugo: 48. Restringido a los robledales noroccidentales. Siempre escaso.

Es la segunda cita tanto para Asturias como para Lugo (Caparrós, Garilleti & Lara 2014).

***Zygodon catarinoi* C.Garcia, F.Lara, Sérgio & Sim-Sim** – Burgos*: 14; Cáceres: 17, 18, 20, 21, 23, 26; Salamanca: 74, 77, 78, 79, 80, 82; Toledo: 95, 96, 99; Zamora: 105. Común en encinares y ocasional en quejigares del occidente de la cuenca del Tajo y del suroccidente de la del Duero; también hallado en un encinar burgalés. De muy escaso a moderadamente abundante (Fig. 5.6g).

Además de ser novedad para Burgos, para Zamora supone la segunda cita provincial (Calabrese & Muñoz 2008). Igualmente, las localidades salmantinas amplían notablemente la distribución conocida de la especie en esa provincia, para la que sólo había una referencia previa (Calabrese & Muñoz 2008).

***Zygodon conoideus* (Dicks.) Hook. & Taylor** – Orense: 68. En un robledal, muy escaso.

***Zygodon rupestris* Schimp. ex Lorentz** – Asturias: 3; Cáceres: 17, 18, 20, 21, 22; Lugo: 48; Madrid: 52; Orense: 68; Palencia: 70; Salamanca: 74, 76, 77, 79, 80, 82; Zamora: 103, 105. Disperso en encinares del occidente de la zona de estudio, siendo más común en la cuenca del Duero que en la del Tajo; también ocasional en los robledales noroccidentales. Generalmente muy escaso o escaso, aunque moderadamente abundante en la localidad del norte de Palencia (loc. 70), que además es el único quejigar en que se ha hallado (Fig. 5.6h).

Es la segunda vez que se indica para Salamanca y Zamora (Calabrese & Muñoz 2008).

***Zygodon viridissimus*(Dicks.) Brid.** – Palencia*: 70. En un quejigar, muy escaso.

5.4 Comentarios al catálogo

El presente catálogo incluye 89 especies de briófitos: 9 hepáticas y 80 musgos. Las hepáticas encontradas pertenecen a 4 familias: Jubulaceae, Lejeuneaceae, Metzgeriaceae, Porellaceae, Radulaceae. La diversidad, así como la frecuencia y la cobertura que muestran las hepáticas en el área de estudio son muy bajas; tan sólo en el extremo noroeste (Asturias, Lugo y las localidades más húmedas de la provincia de León) es frecuente encontrar localidades con varias especies hepáticas que además pueden alcanzar abundancias relativamente altas. En el resto del área de estudio tan sólo *Frullania dilatata* es frecuente como epífita y, en el sector occidental del Sistema Central, puede llegar a ser muy abundante. Por su parte, los musgos resultan mucho más diversos y las especies encontradas pertenecen a 16 familias: Brachytheciaceae, Bryaceae, Cryphaeaceae, Dicranaceae, Ditrichaceae, Entodontaceae, Fabroniaceae, Grimmiaceae, Hedwigiaceae, Hypnaceae, Leptodontaceae, Leskeaceae, Leucodontaceae, Neckeraceae, Orthotrichaceae, Pottiaceae. Entre ellas, Orthotrichaceae (30 especies) y Pottiaceae (19 especies) están especialmente bien representadas. Al igual que sucede en muchas otras áreas del Mediterráneo (Draper *et al.* 2006; Draper, Mazimpaka & Lara 2008; Mazimpaka *et al.* 2009), pertenecen a las Ortotricáceas algunas de las especies más frecuentes y abundantes del área de estudio; destacan en ese sentido *Orthotrichum affine*, *O. diaphanum*, *O. lyellii* y *O. tenellum*. En general, las Potiáceas, aunque diversas, son mucho menos frecuentes y abundantes; tan sólo *Syntrichia laevipila* es una especie muy común, sobre todo en el oeste y sur del territorio, donde además puede llegar a ser notablemente abundante.

En total se aportan 72 nuevas citas provinciales que corresponden a 36 taxones (32 especies y 4 variedades, Tabla 5.2). Aunque no han aparecido grandes novedades corológicas, el estudio supone una aportación significativa al conocimiento de la flora briofítica epífita de la península Ibérica, pues proporciona abundantes datos para diversas provincias poco exploradas, a la vez que completa la distribución de diferentes especies que, por su dificultad de identificación o por su descripción relativamente reciente, han podido pasar desapercibidas. Castilla y León resulta ser la comunidad con mayor número de novedades. A su vez, las provincias que más citas acumulan son Valladolid y Palencia, con 17 y 11 novedades respectivamente (Tabla 5.2). Desde el punto de vista taxonómico, los taxones que resultan novedosos para más provincias son *Hypnum cupressiforme* var. *resupinatum* y *Orthotrichum philiberti*, con 6 primeras referencias provinciales cada una, así como *O. acuminatum*, con 5 nuevas citas

	CLE									E	M	C-LM		
	A	**Bu**	**Le**	**P**	**Sa**	**Sg**	**So**	**Va**	**Za**	**Cc**	**M**	**Cu**	**Gu**	**To**
Antitrichia californica								X						
Brachytheciastrum velutinum								X						
B. velutinum var. *salicinum*		X												
Dialytrichia saxicola										X				
Ditrichum heteromallum		X												
Fabronia pusilla						X								
Grimmia lisae					X		X		X					
H. cupressiforme var. *lacunosum*							X							
H. cupressiforme var. *resupinatum*		X					X	X				X	X	X
H. vaucheri										X				
Neckera pumila				X										
Orthotrichum acuminatum		X	X	X				X	X					
O. affine								X						
O. comosum	X				X			X	X					
O. diaphanum								X						
O. lyellii								X						
O. macrocephalum										X				X
O. pallens							X				X			
O. philibertii	X		X		X			X	X		X			
O. pumilum		X	X	X						X				
O. rupestre								X						
O. schimperi				X				X		X				
O. speciosum				X										
O. stramineum				X										
O. striatum								X						
O. tenellum				X				X						
O. vittii				X										
Syntrichia calcicola								X						
S. laevipila								X						
S. latifolia										X			X	
S. papillosa			X	X						X				
S. papillosissima											X			
S. princeps			X				X	X						
S. subpapillosissima	X													
S. virescens		X		X				X		X				
Tortella inflexa													X	
Zygodon catarinoi		X												
Z. viridissimus				X										

Tabla 5.2: Lista de las especies y taxones infraespecíficos que suponen novedad provincial; las columnas indican las provincias para las que el taxón es novedad. CLE: Castilla y León, E: Extremadura, M: Madrid, C-LM: Castilla- La Mancha. Av: Ávila, Bu: Burgos, P: Palencia; Sa: Salamanca, Sg: Segovia, So: Soria, Va: Valladolid, Za: Zamora, Cc: Caceres, M: Madrid, Cu: Cuenca, Gu: Guadalajara, To: Toledo

Desde el punto de vista taxonómico, los taxones que resultan novedosos para más provincias son *Hypnum cupressiforme* var. *resupinatum* y *Orthotrichum philiberti*, con 6 primeras referencias provinciales cada una, así como *O. acuminatum*, con 5 nuevas citas provinciales. El primero de ellos es una variedad frecuente en el área de estudio pero su identificación entraña dificultades (Ríos & Medina, 2014). En cuanto a *O. philibertii*, es un musgo frecuente en los tramos central y occidental de la cuenca del Tajo, pero su pequeño tamaño, la escasa entidad de muchas de sus poblaciones y la dificultad para diferenciarlo de *O. schimperi* (Lara & Garilleti 2014) han dificultado su hallazgo en diversas zonas del interior peninsular. Pero por otra parte, el que algunas especies comunes y fáciles de identificar, como es el caso de *O. acuminatum*, tengan un número notable de nuevas citas es el signo inequívoco de un conocimiento previo deficiente.

El hecho de que se hayan encontrado numerosas novedades territoriales, aun cuando en varios casos se trata de especies relativamente comunes en estas áreas, apoya la hipótesis de que existe un sesgo en el muestreo y el conocimiento. La parcialidad detectada podría estar originada por la escasez de estudios y la tendencia de los botánicos a herborizar preferentemente en zonas en las que se espera encontrar una alta diversidad o elementos singulares de la flora. Las zonas montanas y las áreas protegidas han recibido mucha más atención que los mosaicos de paisajes agrarios y encinares de las mesetas, y muy especialmente en la Norte. En este sentido, destacamos la importancia de llevar a cabo muestreos sistemáticos que recojan los gradientes ambientales y geográficos en zonas de estudio poco exploradas, de modo que se vayan completando los importantes huecos de conocimiento de la distribución de los briófitos ibéricos.

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CHAPTER

6

Shifts in the importance of species pools and environmental controls of epiphytic bryophyte richness across multiple scales

Abstract Determining the relative importance of local and regional processes has become a focal question in ecology. Using a multi-scale framework we aim to disentangle the relative importance of environmental filters and species pools on species richness of epiphytic bryophytes at different scales. To analyse the across-scale relationships we build a multi-scale framework that relates simultaneously environmental variables with species richness and abundance at three scales: forest (i.e. one measure per locality), stand (i.e. three stands per forest) and tree (a quadrat on a tree, 20 trees per forest). In the proposed conceptual model species pools consist of nested subsets of species of decreasing size that have been filtered through several levels environmental factors. To test whether the data fit the conceptual model we apply a hierarchical structural equation modelling (SEM) approach. We found a strong hierarchical structure in the relative importance of the factors affecting the diversity: forest richness is mostly influenced by environmental variables, but as we decrease the spatial scale the importance of the environment decreases and the dependence on species pool increases. Besides environmental filters at the micro-scale affected locality richness directly and bryophyte cover had a strong relationship with richness at the sample scale. Our results point to the scale dependency of niche *vs.* neutral processes since niche processes have a key role at the forest scale while neutral processes are more significant at the small scale. This together with the importance of abundance for sample richness highlight the need to explicitly address small-scale dispersal processes (i.e. occupancy dynamics) as they might have an important role in shaping species richness. Finally, we propose a modification of the conceptual scheme for the spatial scaling of biodiversity

to accommodate the existence of links across different scales (between micro-environment and forest-scale richness in our study).

6.1 Introduction

One of the fundamental questions of ecology is determining the processes that give rise to local community richness (Elton 1946; Ricklefs 1987; Lawton 1999). Despite decades of intense research, determining the processes that give rise to local community richness remains controversial. During most of the 20th century, research focused on the importance of local factors, mainly species interactions and local abiotic constraints (see for example Elton 1946). However, the realization that factors such as evolutionary history and dispersal constraints were also important led to a more regionally-based perspective (Ricklefs 1987; Harrison & Cornell 2008). Here, much attention has been paid to the importance of the size of the regional pool in constraining local richness. One of the commonest approaches to evaluate this is the regression of local *vs.* regional species richness (see review in Szava-Kovats, Ronk & Pärtel 2013 and references therein).

The relationship between local richness and regional species pool has been seen as an elegantly simple pattern that emerges despite the contingencies affecting it. But the inherent complexity of the factors affecting the local–regional richness relationship is also recognized (Lawton 1999). Critical reviews of the theoretical grounds of local to regional species richness regressions have shown that the ecological processes cannot be discerned based solely on local–regional richness regression (Szava-Kovats *et al.* 2013). Hence, to move forward in this debate it is necessary to take into account the set of intermingled mechanisms operating at several spatiotemporal scales that influence richness patterns under a multi-level framework (Ricklefs 1987; Harrison & Cornell 2008). In this regard, a rewarding approach has been based on considering that communities are successively filtered into decreasingly smaller species pools by a nested set of multi-level, hierarchically structured environmental filters (Keddy 1992; Pärtel *et al.* 1996; Rajaniemi 2003; Guisan & Rahbek 2011; Sydenham *et al.* 2015).

A structural equation modelling (SEM) allows the evaluation of this type of multivariate hypotheses (Harrison *et al.* 2006; Harrison & Cornell 2008) and the testing of simultaneous influences and responses. For example, the regional pool can be simultaneously modelled as a response variable in relation to environment and as the predictor of local richness. Also, SEM tests hypothesized *a priori* model

structures in addition to individual coefficients, so it can be used to validate conceptual frameworks.

In this work we study bryophyte communities growing on evergreen oak (*Quercus ilex* L.) trunks in the northern and central inland Iberian Peninsula. Bryophytes offer a number of advantages as focal organisms in ecological research. They are primarily a spore-dispersing group in which dispersal units can normally travel long distances due to their small size, so no dispersal limitation is expected at small scales (but see Löbel & Rydin 2009). Besides, due to their small body size and the lack of active regulation of internal water content, these plants are thought to be strongly dependent on the small scale environment (Ingerpuu *et al.* 2003; González-Mancebo, Losada-Lima & Llorente 2004; de Oliveira *et al.* 2009), so they are useful model organisms to detect the importance of environmental filters at several scales. Despite their adequacy as model organisms and their globally near-ubiquity, tests for local–regional richness relationships in bryophytes are very scarce, and these have largely been constrained to one ecosystem type, peatlands (During & Lloret 2001; Rydin & Barber 2001).

Our main goal was to investigate the effect of environmental filters and species pools on species richness of epiphytic bryophytes at different scales. Specifically, we aimed to test to what extent the effect of the species pool is transmitted through the scales and how big is the impact of the species pool in comparison with environmental filters. To do this, we propose an *a priori* model with different levels of environmental filters, and three scales of biotic measures that describe the hypothesized drivers of species richness in bryophyte communities (Fig. 6.1, and Fig. D1 in the supplementary material). The general structure of the model is contextualized within current theoretical frameworks for the effects of filters and processes acting at different scales (Whittaker, Willis & Field 2001; Hortal *et al.* 2010; Guisan & Rahbek 2011), while the specific relationships are founded on previous empirical knowledge based on simpler analyses on cross-scale bryophyte richness patterns (Medina *et al.* 2014).

6.2 Methods

Study area

The study was conducted in the north and center of inland Spain, covering more than 150,000 km^2 and almost 1/4th of the Iberian Peninsula. The area includes the Duero and Tagus basins within the Spanish territory and three major mountain

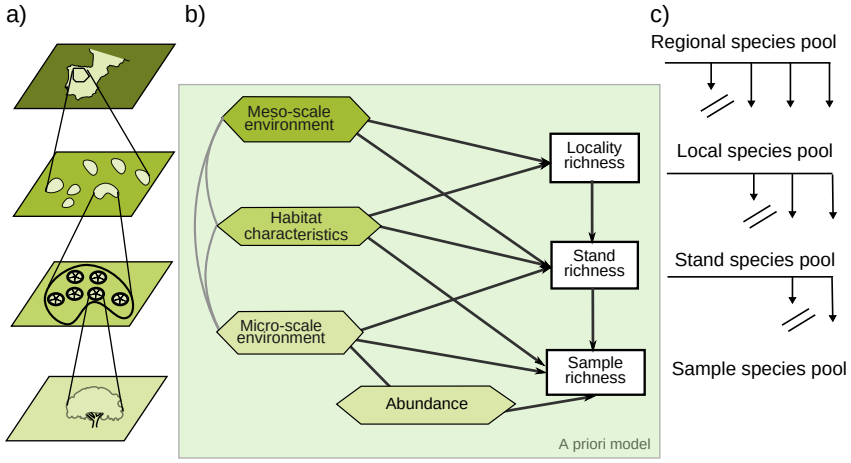

Figure 6.1: Conceptual model of the hypothesis about the relationships between bryophyte richness and abundance at several scales and environmental predictors. a) Representation of the analysed environmental scales showing the nested structure of the data. b) Simplified *a priori* model showing the groups of environmental variables and the expected links between them. Arrows indicate hypothesized links, curved arrows represent correlations. c) Hypothetic cross-scale filtering of the species pool. The initial pool of species is successively filtered by the different factors, note that richness at each scale represents the species pool for the level immediately below

ranges, namely the Central Mountain range, the southern slope of the Cantabrian Mountains, and the western slope of the Iberian Mountain System (Fig. 6.2). Climate in the study area is Mediterranean, covering an important precipitation gradient: annual precipitation in the studied *Quercus ilex* forests precipitation varies from 363 to 776 mm. There is also a large gradient in the range of variation of extreme temperatures since the area hosts suboceanic zones with relatively small annual temperature changes and others, in the inner Northern Iberian Plateau, that represent the extreme of continentality within the Mediterranean climate. The landscape is a mosaic of crops, urban areas and forested patches. The study focuses on evergreen *Quercus ilex* L. forests, one of the commonest types of woody vegetation in the area. Forest structure varies between open *dehesas*, which consist of semi-natural wood-pastures interspersed with croplands and Mediterranean scrubs where trees with large average diameters dominate and scrub cover is generally low, and closed forests composed of trees of varying diameters with a more or less diverse shrub layer.

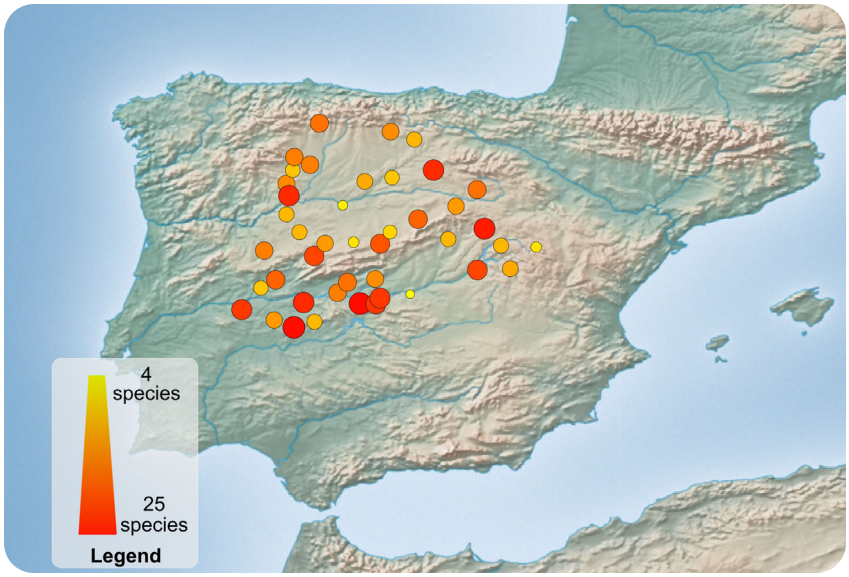

Figure 6.2: Map of the Iberian Peninsula showing the 43 sampled localities. Color and size of the dot is related to richness of the forest, darker and bigger dots being the richest localities

Sampling design

The sampled forests were selected in order to maximize the coverage of environmental and spatial variability within the studied territory. A complete description of the survey design can be found in Medina *et al.* (2013). Overall, we studied 43 *Quercus ilex* dominated forests.

To characterize each forest, we examined aerial photographs and explored the forest to locate and select three stands with homogeneous conditions and separated by at least 100 meters that represented the overall structure of the forest. Each stand was divided into four sectors of 45 degree arcs using the geographic North as a reference (D2, supplementary material). Tree-scale characteristics were measured in the four trees closest to the center in each sector, and stand-scale characteristics were based on the circular area that includes the six closest trees.

We gathered 20 samples in each forest, seven samples in each of the first two stands and six in the last one. Each sample consisted of a quadrat of 400 cm^2 taken on a tree trunk at a height within the interval of 1.20-2.00 m above the ground. Such height avoids an excessive influence of the colonization of soil bryophytes (occasional epiphytic species, *sensu* Mazimpaka & Lara (1995) and ensures the comparability of the sampled communities. Samples were taken always on the side of the tree with the highest bryophyte cover. Tree diameter was between 10 and

50 cm (DBH). Since not all trees in a forest are colonized by epiphytic bryophytes, when necessary we extended the surveys to gather 20 samples with bryophytes, or up to 100 visited trees. We also counted the number of examined trees that had no bryophytes.

Environmental variables

The effects of environmental filters occur in a set of nested scales. Here we study three different levels: meso-scale, habitat scale and micro-scale; and we classified the environmental filters according to this scheme (see Table D1, supplementary material). Some effects occur clearly on one of these levels (climate is unambiguously measured at the meso-scale) but in other cases the definition of scale is not so clear. For example, forest management can change at the landscape scale and within localities depending on the specific characteristics of the study site. Although the classification into one or other level is not unequivocal we have tried to capture the most important gradients within each scale of analysis in our study area. As described in Table D1 (supplementary material), the *meso-scale environment* was characterized by four variables grouped into two subcategories: climate and topography. *Habitat characteristics* include two subcategories; forest management and forest structure. Forest management was measured for each forest because the two variables included in this category (forest history and forest percentage) are related to landscape scale variation and are more or less homogeneous within each forest patch. On the contrary, the two variables describing forest structure (canopy cover and tree density) change within localities and across stands. The *micro-environment* was characterized by four variables measured characteristics known to affect bryophyte communities (see e.g. Barkman 1958; Löbel, Dengler & Hobohm 2006; Király *et al.* 2013), three describe tree characteristics and one describes the amount of light that penetrates through the canopy.

Biotic variables

We calculated three different richness measures at the forest, stand and sample scales: (1) Forest richness, as the total number of species gathered in all samples of a forest (usually 20 samples, but note that we took less samples in 15 forests due to low colonization, so several samples were assumed to have no epiphytic bryophytes); (2) Stand richness, as the total number of species on all the samples in a stand (129 stands in total: 3 stands x 43 forests); and (3) Sample richness, as

the number of species in each 400 cm^2 quadrat; as environmental variables were measured only for 12 trees in each forest (4 trees per stand), we only considered these trees in the analysis of sample richness. Note that for this latter scale some of the trees lacked bryophytes, so the richness of these samples was assigned to zero. We also calculated bryophyte cover at the sample-scale as the percentage of the surveyed 400 cm^2 tree-trunk area that was covered by bryophytes. The total number of samples considered at this smaller level was 516 (4 samples x 3 stands x 43 forests). In some cases, the information of the samples was incomplete for different reasons (i.e., we were unable to record some variables, light transmission images were damaged or bryophyte samples were lost). The samples with missing values in one or more fields were deleted, so the final number of analysed samples was 467.

Finally, we calculated the strength of dominance shown by the most common species by calculating the mean commonness of the commonest species. To quantify the commonness of the species in each forest we used h_p index (Arellano *et al.* 2014), a metric based on h citation index that assesses the proportion of samples (h_p) where the species is present with a cover higher than h_p. For example, a species with h_p of 20 in a given forest will be covering 20% or more of the surface of the quadrats of 20% or more of the samples from that forest.

Data was collected in several campaigns between August 2009 and March 2013. Samples were identified to species level in the laboratory. The species list can be found in Table D2 (supplementary material). Nomenclature follows Ros *et al.* (2007) for liverworts and Ros *et al.* (2013) for mosses.

Statistical analyses

We used Structural Equation Modelling (SEM) to evaluate the relative importance of the environmental variables and species pools. This statistical method is used as a confirmatory technique by formulating an initial hypothesis.

The hypothesized model is represented as a graphical model of relationships and translated into a composite set of mathematical hypotheses. The model is then tested against experimental or observational data. The assumption evaluated is that the structure of correlations of the empiric data is not statistically different from the structure of correlations expected from the hypothesized model (i.e. initial model). Very often this initial model requires some adjustments to make it compatible with the structure of relationships in the data. In these cases, the model is modified by adding new relationships until it becomes compatible with observed data. When

a model fits a dataset, this indicates that the model is a plausible causal scenario that could account for the covariance structure of the dataset; however, it does not indicate that a model is the best fitting of all possible models or the only good fitting model.

Classical SEM used in previous works on the local–regional richness relationship (Harrison & Cornell 2008) have some limitations when applied to the analysis of this relationship, as it does not take into account the inherently nested structure of the data. To overcome this problem we applied a recently developed method: the d-separation test (Shipley 2000). This test is very flexible and can be used in combination with mixed effects models to tackle the hierarchical structure of the data. Briefly, every SEM implies predictions about which variables will be (conditionally) independent (Shipley 2000). The d-separation test is based on determining the dependence or independence of any pair of variables after statistically controlling for (i.e. holding constant) the rest of the variables. This is equivalent to looking at the slope of a regression in a mixed model with multiple variables (Shipley 2009). To apply the d-separation test we must first define the minimum set of pairs of variables that need to be uncorrelated if the *a priori* model is correct (see Shipley 2000, 2009 for a detailed definition of the basis set), to then test simultaneously all the independence claims. The null hypothesis of this test is that the model is compatible with the data, so significant values imply a poor fit. The d-separation test also allows identifying potential changes that will likely produce fit improvement (new paths). We modified the model adding new paths until the fit was not significant. Finally, when we achieved a model that was compatible with the data, we calculated the path coefficients (regression coefficients). For the sake of clarity and repeatability we provide a detailed description of the steps followed to apply the technique to our data and the corresponding R scripts in Appendix D.1, supplementary material.

6.3 **Results**

Overall, we recorded 57 bryophyte species in the study area (Table D2, suplementary material). Each forest harbored between 4 and 25 species. At the stand-scale, species richness varied between 0 and 21 species, while at the sample-scale it varied between 0 and 13. Average bryophyte cover value was 27%. The overall fit of the SEM model was adequate after some modifications (p=0.28). We added four new relationships to the initial model in order obtain a satisfactory fit; the relationships that were included linked micro-scale characteristics (bark roughness and diameter)

and bryophyte cover to forest richness, and forest richness to sample richness. For simplicity, we present the results of the fixed effects that had a significant effect on any of the endogenous variables ($p<0.05$). Table D3 in supplementary material provides the results of both fixed and random effects and a detailed table including unstandardized coefficients, t-values and standard deviation of coefficients.

The model explained 27% of the observed variability in forest richness. The environmental filters at the meso- scale and micro- scale contributed to explain this variability (Fig. 6.3). At the meso-scale, annual mean temperature and slope were the only relevant variables, annual mean temperature contributed with a relatively large path coefficient (0.22) compared to slope (0.11). Habitat characteristics had relatively small effects, within this group forest percentage showed a negative effect (-0.10) and open forest with a positive one (0.12). At the micro-scale, bark roughness showed a positive effect (0.19) while diameter showed a negative effect (path coefficient =-0.28). Finally, bryophyte cover (abundance) had a strong positive effect (0.26).

At the stand scale, the fixed effects explained a low amount of variability in species richness (14%; Fig. 6.3). Meso-scale environment was not significantly linked to stand richness. Rather, habitat characteristics showed a significant effect as tree density negatively influenced stand richness (path = -0.17). The micro-scale environmental variables also had a significant effect on stand richness, in particular tree diameter, which was negatively correlated (-0.11), and canopy depth, which was weakly and positively linked to it (0.07). The largest effect (0.71) was that of forest richness, which explained most of the observed variability in stand richness.

At the sample-scale the fixed effects explained up to 50% of the observed variability (Fig. 6.3). The effect of environmental variables on sample richness was very small; only forest history (open forest) had a significant but small effect (-0.11) on sample richness. The rest of the environmental variables at the meso-, habitat- and micro-scales had no significant effects (although percent forest and canopy cover had a marginally significant effect, see Table D3 in supplementary material). Instead, the strongest paths linked sample richness with bryophyte cover (0.53), stand richness (0.19) and forest richness (0.23).

Finally, the fixed effects explained 21% of the variability in bryophyte cover. The most important factors were linked to habitat characteristics and micro-scale environment (Fig. 6.3). The most influential habitat variable was canopy cover with a positive coefficient (0.22). Trunk diameter also showed a strong effect (0.27).

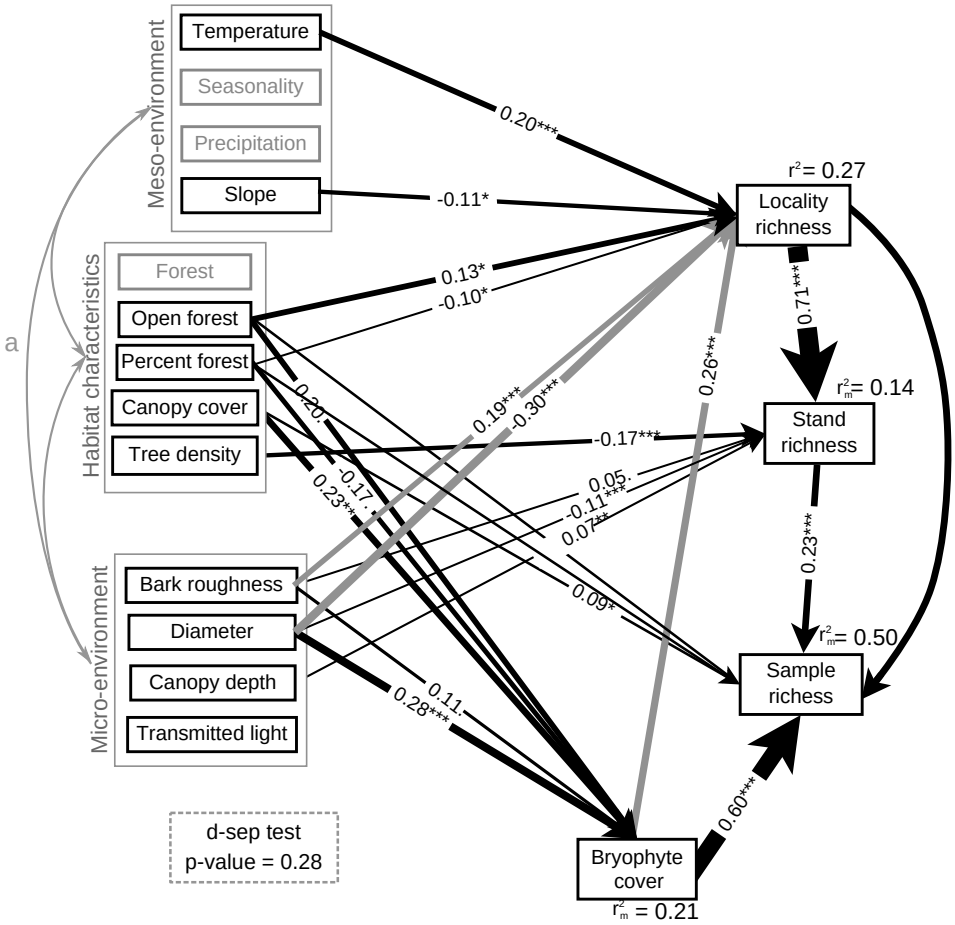

Figure 6.3: Results of the SEM analysis showing all significant paths (the complete result with all considered paths can be seen in Fig. D1 and Table D3 in supplementary material). Numbers in lines indicate standardized coefficients. Black boxes indicate variables with a significant relationship with at least an endogenous variable while grey boxes indicate variables with no significant correlation with any of the endogenous variables. Grey curved arrows indicate groups of variables that were allowed to correlate (see Table D4 in supplementary material for actual correlations among variables). Grey straight arrows are links added during the model fitting process while black arrows are links present in the *a priori model.* The initially hypothesized *a priori* model is depicted in Fig. 6.1 and a complete model with all the considered paths including the correlations between exogenous variables can be found in Table D4, supplementary material.

6.4 Discussion

Importance of the size of the species pool

Our results provide evidence that the size of the species pool has the largest influence on richness of epiphytic bryophytes, an effect that changes in importance with

scale. This strong top-down structure in which the species pool effect is predominant follows the same overall structure found by Medina et al. (2014)[1] for a different host tree and region (compare our Fig. 6.3 with their Fig. 6[2]). The high importance of the species pool indicates that environmental conditions alone are not sufficient to explain observed richness patterns. Although this is not a direct proof of the importance of dispersal effects, strong relationships between species pool and richness when environmental effects are controlled have been related to propagule supply (Cornell & Harrison 2013). Therefore it can be argued that our results point to dispersal effects (i.e. neutral processes including colonization and local extinction, dispersion and migration) as major drivers of the diversity of epiphytic bryophyte communities. Nonetheless, environmental variables also contribute to explaining richness, so both neutral and deterministic processes seem to jointly structure the epiphytic communities in the study area. This supports the argument that, rather than being mutually exclusive, neutral and deterministic hypotheses represent extremes in a continuum (Gravel *et al.* 2006; Legendre *et al.* 2009).

Scale dependency of the effects

Our results also show a gradient in the relative importance of the effects of environmental filters and the size of species pools across scales. While forest richness is constrained mainly by environmental filters, stand richness is influenced by both environment and species pools, and sample richness is constrained mainly by species pools with only a small direct effect of environmental filters. Previous work has also shown that the balance between neutral and deterministic factors is scale-dependent. Studies analyzing effects across scales also suggest that the importance of neutral processes increases as scale diminishes (Karst, Gilbert & Lechowicz 2005; Legendre *et al.* 2009). That is, forest richness is more related to deterministic factors while sample richness seems to be more related to neutral processes. This change in the relative importance of neutral *vs.* deterministic factors with scale may be partially responsible for the contrasting results found in the literature of bryophyte richness with some studies highlighting the importance of meso-scale environment (Vitt, Li & Belland 1995; Zechmeister *et al.* 2003; Pharo *et al.* 2005; Callaghan & Ashton 2008; Raabe *et al.* 2010), and others pointing at micro-scale environment being more relevant (Humphrey *et al.* 2002; Bacaro *et al.* 2008; Hespanhol *et al.* 2011).

[1] Chapter 2 in this thesis
[2] Fig. 2.6 in this thesis

Although the overall importance of regional richness for forest diversity and the scaling down of the effects of species pool and environment seem to be general for epiphytic bryophytes, some unexpected results arise from our final model. Perhaps the most surprising is the direct link between small scale variables and forest richness. We designed our initial hypothesis following general theoretical schemes which link environmental variables at different scales with richness at more or less equivalent scales (Whittaker *et al.* 2001; Guisan & Rahbek 2011). That is, meso-scale environment would be linked to forest and stand richness, and micro-scale environment would be so to sample and stand richness. However, contrary to our expectations several micro-scale environmental variables directly affected richness at the forest-scale (see Fig. 6.3). Further, bryophyte cover (i.e. abundance) shows strong significant effects not only on sample species richness, but also at the forest-scale. We therefore propose a modification of the conceptual scheme for the spatial scaling of biodiversity proposed by Guisan & Rahbek (2011) that accommodates to the cross-scale effects observed in our study (Fig. 6.4). Whether this scheme is more general or simply contingent on the organisms and region under study deserves further investigation. However, our results provide evidence that, despite their overall applicability, simple schemes of the scaling of environmental and biotic effects may not be general enough to represent spatial variations of diversity at the finer scales, at least for some groups. Rather, the complexity of the processes involved at different scales may require including several reversions of the general top-down scaling path depicted by Whittaker *et al.* (2001) or Guisan & Rahbek (2011), if the aim is to provide a fine-grain integration of the spatially-explicit processes acting at the metacommunity level. In fact, the (arguable) pre-eminence of neutral processes at the sample-scale and the effects of sample bryophyte cover at the forest-scale may point to the effects of occupancy dynamics (i.e. stochastic spatially-structured metapopulational and dispersal processes; see Hortal *et al.* 2010) as a major component of the scaling of species richness, at least up to local scales. Our results seem to support the idea that besides large biogeographic dispersal effects, small scale dispersal processes (i.e. occupancy dynamics) need to be explicitly addressed. For individual dispersal movements, population dynamics and metapopulation processes might be determining the degree of aggregation of populations and ultimately the number of coexisting species at least at fine grained scales.

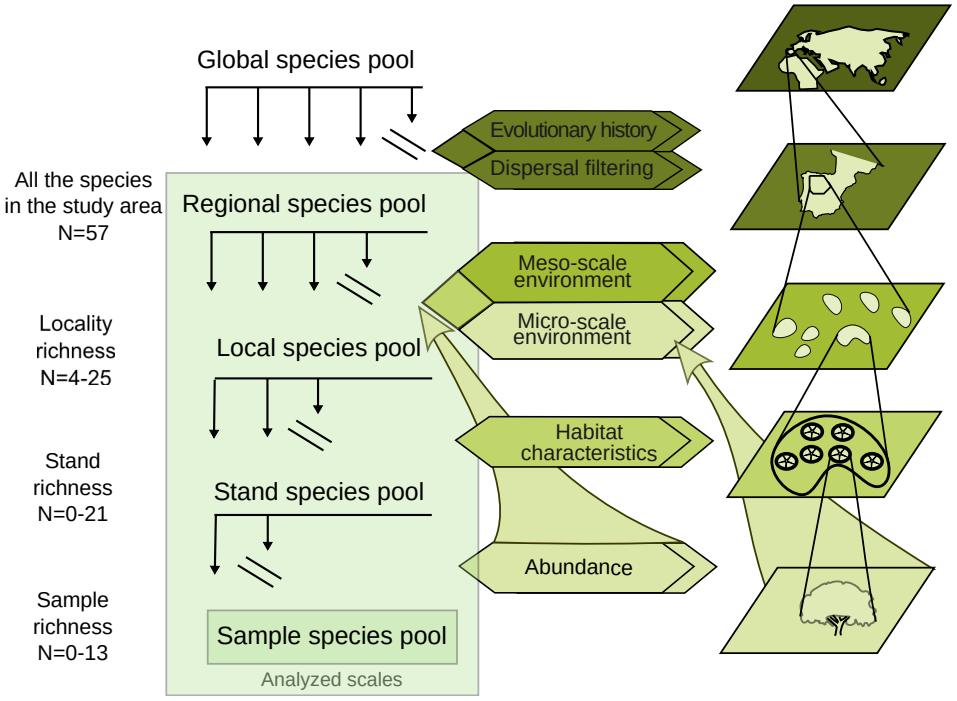

Figure 6.4: Summary of the main factors filtering species pools at the different scales. Based on the general scheme in Guisan & Rahbek (2011) (see also Fig. 6.1). Abundance and micro-scale environment show effects on larger scales filtering the species pool at the regional scale

Environmental filters

The in-depth analysis of the environmental filters allows evaluating the degree of coherence of the particular links within the general scheme and the degree to which idiosyncratic effects might be influencing our results. The presence of relevant effects of meso-environmental filters and habitat characteristics on forest richness is a well-supported pattern (Vitt *et al.* 1995; Pharo *et al.* 2005; Király *et al.* 2013; Medina *et al.* 2014). However, the sign and size of the effects seem to be more idiosyncratic. In our results, the most relevant environmental filters include climate and topography. Surprisingly, from the analyzed climatic variables only mean annual temperature has a strong influence on forest richness. This contradicts previous work showing that both precipitation and temperature are important for epiphytic bryophytes (Medina *et al.* 2014) and contrasts with the general idea that water availability is the main limiting factor of diversity in Mediterranean climates (Font i Quer 1954). This unexpected result may be due to the idiosyncrasy of the study area, where the large continentality gradient (e.g. increased range of temperature

in the inner continental zones of the study area) may overrule the effect of precipitation, or to differences in study area extent, which are known to result in changes in the importance of climatic factors (Aranda *et al.* 2013).

The unexpected direct effect of small scale environment (bark roughness and diameter) on forest richness might be pointing to the importance of habitat heterogeneity for species diversity. In accordance with this hypothesis, we find a linear increase in variability in relation to the average of bark roughness and transmitted light on each tree trunk (Spearman rho = 0.57 and 0.52 respectively). Similar results highlighting the importance of habitat heterogeneity have been repeatedly found in a range of organisms and regions (Stein, Gerstner & Kreft 2014), including bryophytes (Rambo 2001; Gignac & Dale 2005). More surprising is the negative link between diameter and forest richness. Several, non-mutually exclusive hypotheses can explain this pattern. First, decreasing richness of epiphytic bryophytes with diameter has been attributed to competitive exclusion during succession (see e.g. Mazimpaka *et al.* 2010; but see Lara & Mazimpaka 1998; Király *et al.* 2013; Flores-Palacios & García-Franco 2006). However, this seems unlikely in our study system as there is no significant relationship between average diameter and dominance (Spearman correlation= -0.1, p= 0.58). Second, the low habitat heterogeneity of the *dehesas* in the study area (which are constituted mainly by large diameter trees) might be conditioning the shape of the relationship between diameter and richness (see Fig. D3, supplementary material). Third, it might be possible that some unmeasured factors such as the chemical, physical or other conditions of the trees prevent coexistence so that less species are capable of colonizing old trees. Unfortunately this cannot be addressed with our data.

Stand richness represents an intermediate scale where both environmental filters and species pool have important effects. Here, a strong influence of site specific random factors was detected. Note however that, although the fixed effects of the model explained just 14% of the variability, total r^2 was high (97%). The fixed effects with the highest impact on stand richness were mainly canopy depth and diameter, the latter with a negative effect (Fig. 6.4). Similar to the pattern observed in forest richness, these results evidence a relationship between habitat heterogeneity and richness also at this scale.

For sample richness, there was no direct link with micro-scale environment. Most of the explained variability was linked to either the species pool effect or bryophyte cover on each tree trunk (Fig. 6.3) which together explained a high proportion of sample richness variability (up to 50%). The lack of importance of

micro-scale environment is surprising as previous work on bryophyte communities has emphasized its relevance (Bacaro *et al.* 2008; de Oliveira *et al.* 2009; Hespanhol *et al.* 2011). In fact, we included four microclimate descriptors that had previously been reported to be important for epiphytic bryophytes (see e.g. Barkman 1958; Löbel *et al.* 2006; Király *et al.* 2013) and were therefore expecting to detect an effect of environmental filters at this scale. Interestingly, there is a strong indirect effect of environmental filters on sample richness mediated by abundance. Bryophyte cover is mostly influenced by habitat and tree characteristics and is one of the most important predictors of sample richness, so environmental conditions are indirectly constraining richness through their effect in bryophyte cover. The generality of this indirect effect is unknown since none of the studies dealing with richness-environment relationships in bryophytes simultaneously analysed cover and richness.

Importance of bryophyte abundance

The links that relate sample-scale bryophyte cover to forest and sample richness deserve further attention as they represent a core set of relationships within the studied system. Biotic interactions have been invoked as key processes that shape the link between bryophyte cover and richness (see e.g. Grime 1973; Klanderud 2010). Hypothetically, in a saturated community, competition may play a relevant role by limiting coexistence (Cornell & Lawton 1992). However, this is hardly the case for epiphytic bryophyte communities in the studied area, as trunk bryophyte cover is relatively low (average bryophyte cover *ca.* 27%). Hence, in the harsh environment that characterizes the study area the effect of environmental filters and the species pool are likely to have a higher impact on richness than competition. The strong link between sample bryophyte cover and richness at the two scales (forest and sample) together with the strong effect of the species pool might be pointing to a key role of population size and propagule supply in maintaining richness. Here, more individuals imply lower extinction risk and higher probability of successful colonization in an environment where efficient dispersal is crucial for maintaining bryophyte populations as trees represent dynamic and isolated favorable patches in a matrix of mostly unsuitable environment (Löbel & Rydin 2009). Also small-scale heterogeneity might be promoting coexistence at both forest and tree scales. The micro-environmental differences between tree trunks will allow the establishment of species with different requirements, which will find optimal conditions (and therefore produce more propagules) in several of them. This, together

with lower competitive pressures derived from the wide availability of free trunk space, would allow maintaining populations of many species even if conditions are suboptimal.

6.5 Concluding remarks

We advocate the validity of multi-level models based on the idea that diversity is successively filtered through several processes organized in a nested set of hierarchical scales. The study of local–regional richness relationship within this multi-level framework can contribute to fill in the gaps in knowledge and better understand the most likely causes of diversity at each scale. We found a strong hierarchal structure in the relative importance of the factors affecting the diversity of epiphytic bryophyte communities under a Mediterranean climate: forest richness is mostly influenced by environmental variables but as we decrease the spatial scale of our observations, the importance of the environment decreases and the dependence on species pool increases. Although we don't have direct evidence about the prevalence of either niche or neutral processes, our results point out to niche processes as principal determinants at the forest-scale and neutral processes as principal determinants at the smallest scale with bryophyte cover as a key mediator. Here, a strong correlation between species richness at the sample-scale and environment arises from the transmission of the environmental effects through species pool and bryophyte cover.

The generality of the intricate network of relationships across scales we found here needs to be evaluated in other communities to determine whether it is a consistent pattern. Also, further confirmation of the hypothesized mechanisms should be sought in composition changes in communities. The relationship between local and regional richness is directly connected to species turnover since lower local richness with similar values of regional richness implies a higher spatial turnover (Srivastava 1999; Loreau 2000; Belmaker *et al.* 2008). Here, as species turnover is tied to species identity the relationship between local and regional richness is closely associated with understanding species composition patterns.

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CHAPTER

7

Biogeographically distinct regions show different patterns of across scale environmental filtering

Abstract Understanding the determinants of beta diversity patterns is a central issue in Ecology since beta diversity has been recognized as a benchmark that may help to connect processes with patterns. In this work we study how differences in the pool of colonizers, environmental conditions and geographic distance determine changes in species composition of epiphytic bryophytes across two scales of analysis (forest and tree). First, we identify biogeographic modules of co-occurring species (i.e chorotypes) across the territory using network analyses, and evaluate the consistency of these modules across scales. We found four main chorotypes from which the one spanning through the Atlantic region outstand because of its consistency across measures and scales. Then we study the changes in the importance of environmental (niche) filters on beta diversity across scales. This allowed us to identify the structuring of epiphytic bryophyte communities as a by-product of the balance between niche-related and neutral processes. This balance that changes with space and scale so that neutral stochastic effects are larger in the most favourable regions and increase as the scale decreases. Neutral and niche processes represent intrinsic parts of community assembly, their balance varies across scales in a structured way that depends on the spatial dynamics of each group, the environmental variability of the region and the species present in the pool of potential colonizers.

7.1 Introduction

Understanding the mechanisms behind diversity patterns is a pressing issue, necessary to understand ecological and evolutionary processes, inform on conservation actions, and project ecosystem responses under different global change scenarios. Perhaps due to its complexity, the analysis of beta diversity patterns has drawn much less attention than the study of species richness. However, beta diversity has been recognized as a benchmark that may help to connect processes with patterns, since it explicitly takes into account the identities of the species (Baselga & Orme 2012; Chave 2013). Here, several complementary sets of hypotheses have been invoked to explain beta diversity patterns, including niche and neutral theories. Niche theory suggests that changes in community composition are tied to the ability of the component species to adapt to the abiotic environment and to compete for the available niche space (Keddy 1992). As a result differences in community composition should be related to environmental variability. In contrast, according to neutral theory all the individuals of the same guild present in a community are ecologically equivalent, so changes in community composition rely solely on dispersal processes (Hubbell 2001). This implies that the identity and relative abundances of the species present locally are the result of demographic stochasticity, so beta diversity patterns would be only determined by the relative abundances of the species in the regional pool and the local community (Hubbell 2001). Rather than being mutually exclusive, neutral and deterministic processes represent extremes in a continuum that may be operating simultaneously in a community depending on the conditions (Gravel *et al.* 2006; Legendre *et al.* 2009). Thus, the key question becomes identifying under which circumstances one or the other mechanism is dominant (Siepielski & Mcpeek 2013).

Several studies have shown that the relative importance of the factors affecting diversity patterns is scale dependent (see for example Field *et al.* 2009; Shipley, Paine & Baraloto 2011). Most of these studies indicate that the strength of the environmental filters increases at larger scales, such as, e.g., for the diversity of epiphytic bryophytes in Mediterranean climates (2014). Besides, the relative importance of the factors structuring diversity may differ between biogeographic regions (see for example Myers *et al.* 2013). In regions with large environmental differences, ecological drift will be mostly preeminent in benign environments, where –in theory– the majority of the species from the regional pool can colonize local communities (Chase 2007). In these situations, community composition across localities with similar environmental conditions and limited resources would

be highly variable due to stochastic colonization processes. This could be the case of tropical forests or coral reefs, where the best evidence of the neutral theory has been found (Hubbell 2001; Condit *et al.* 2002; Volkov *et al.* 2007). In contrast, under harsh conditions most of the species from the regional pool are filtered out by the environment, so less species are able to colonize the site. (Chase 2007). As a consequence, community composition of localities with similar environmental conditions will be more homogeneous, making community structure more prone to show niche-assembled structure (Chase 2007).

In this work we study how differences in the pool of colonizers, environmental conditions and geographic distance determine changes in species composition. We do this using data from a multi-scale standardized survey of epiphytic bryophyte communities in the northwestern region of continental Iberian Peninsula (Medina *et al.* 2015). First, we identify biogeographic modules of co-occurring species (i.e chorotypes) across the territory using network analyses, and evaluate the consistency of these modules across scales, from the species inhabiting a tree to those present in a whole forest (objective 1). Then we study the changes in the importance of environmental (niche) filters on beta diversity across scales and modules (objective 2), trying to identify the situations in which environmental filters are prevalent. To do this, we first evaluate whether the strength of the environmental filters varies across modules (objective 2a). Here, we expect that the relative importance of these filters will change according to increasing harshness, so if we are able to detect significant modules, we will also find strong differences in the importance of the environmental filters across modules. We hypothesize that the modules characterized by harsher conditions will show stronger environmental filtering effects, while modules in favorable environments will have a stronger effect of ecological drift and a therefore smaller contribution of environmental filters. Finally, we test (objective 2b) whether there are changes in the strength of environmental filtering between tree and forest scales. Here, we expect environmental filtering to be less important as scale decreases.

7.2 Material and Methods

Study area and data

The study was carried out in the North and Center of continental Spain, approximately within 39º 15' – 43º 16' N and 1º 47' – 7º 35' W (Fig. 7.1a). The study area is characterized by a complex topography, with elevation ranges between less

than 200 m a.s.l. in the Tagus basin, close to the border with Portugal, to over 2000 m a.s.l. in the mountainous areas. Besides, there is a strong climatic gradient from areas with more or less dry Mediterranean continental climate in the northern and southern plateaus, to an area with an Atlantic climate, characterized by wet summers and relatively mild winters, in the northwest. We studied a total of 107 forests that were explicitly selected to be representative of the environmental and geographic gradients (see Medina *et al.* 2013). Each forest was surveyed placing 3 stands separated by at least 100 meters and taking 20 samples of bryophytes per forest (7 samples in two of the stands and 6 in the third one) whenever possible (Medina *et al*. 2015). Each sample consisted of a 400 cm^2 quadrat taken off trees with diameters between 10 and 45 cm at a height between 1.20 and 2 meters in the side of the tree with the highest bryophyte cover. Percentage of bryophyte cover in the quadrat was assessed before sample removal so that the cover of each species could be estimated in the laboratory based on the relative abundance of the species in the sample. Four matrices describing community composition were derived from these data: two presence-absence (binary) matrices –one at sample (tree) scale and the other at locality (forest) scale– and two abundance based matrices –also at sample and locality scales–. Additionally, we measured the commonness of the species in the community using the h_h index (Arellano *et al.* 2014). This index measures the average commonness of the commonest species. Here, commonness is measured on the basis of the h index that assesses the proportion of samples (h_p) where the species is present with a cover higher than h_p. For example, a species with a h_h index of 20 will be present in 20% of the samples at least with a 20% cover.

Environmental conditions were characterized by three groups of predictors (see Appedix E.1 and Fig. E1 in supplementary material for a detailed description): meso-scale abiotic environment including climatic and topographic variables; habitat characteristics measured at stand scale (three stands per forest, the values of the variables are averaged per forest); and micro-scale environment measured at tree scale (we selected 4 trees per stand, twelve trees per forest). Besides these variables we also calculated the environmental heterogeneity both in habitat characteristics and micro-scale environment.

Statistical analyses

Network analyses

We used a co-occurrence network approach to study the structure of the variations in species composition (objective 1). We did so by characterizing compositional similarities through modularity analyses based on binary and abundance data at the two scales of analysis (forest and tree). Hence, the final output consisted of four different analyses, one for each combination of scale and type of data. The aim of these analyses is to identify groups of sites sharing species which, in turn, are more often distributed within these sites (i.e. regions and their species pools). Here, species co-occurrence networks are considered as bipartite networks, where sites and species constitute two subsets of nodes and links depicting species presences into sites (Thébault 2013), being the weight of the link determined by species abundance in the case of abundance based networks. In general, modularity analysis is directed to find the partition (i.e. the ensemble of groups or modules) that maximizes the number of links within modules (or their strength in weighted networks) while minimizing the number of links between modules (Newman 2004). Here we used a modularity index that was specifically designed for bipartite networks (Barber 2007; see also Thébault 2013) and the Louvain optimization algorithm (Blondel *et al.*, 2008) as implemented in the function GenLouvain (Mucha *et al.* 2010 available at http://netwiki.amath.unc.edu). Given the heuristic nature of the analyses, the obtained partition may result on local optima so we repeated the analysis 100 times and selected the partition with the highest modularity value.

Once a modular partition of the network is selected, network analysis also provides a way to measure attributes of particular species (or sites) within the network (Carstensen *et al.* 2013). Species attributes or roles in the network are defined by two indicators. The first indicator (intra-modular connectivity) describes how well a species or a site is connected with other nodes within its module. This index takes positive values for highly connected nodes and negative values for isolated ones. The second indicator (inter-modular connectivity) measures the distribution of the species across modules. This index takes a value of 0 when the species is exclusive of a module while it tends to 1 when the species is equally distributed across all modules. The two indices define a two-dimensional space that can be divided assigning different roles to each subspace within the graph (Fig. 7.2). In our case, the divisions were set after Guimerà & Amaral (2005) and Carstensen (2013). See Appendix E.2, supplementary material for a complete explanation and a numerical description of both indicators.

Relationship of species composition with environment and commonness

Taking into account the correspondence of patterns across measure types and in the sake for clarity all the analyses of this section were done only with binary data.

Within forest beta diversity

We calculated the total dissimilarity among the trees within a forest with the multiple-site beta diversity measurements implemented in the betapart package (Baselga & Orme 2012; Baselga 2013) on R (R Development Core Team 2011). We calculated both β_{sim} and β_{nes} that respectively account for the turnover and nestedness components of the Sorensen index (Baselga & Orme 2012).

We used linear regressions to identify the best predictors of within-forest beta diversity. The selection of predictors was done in two steps. To avoid multicollinearity we first performed a preselection of the climatic variables using individual regressions with beta diversity indices for each variable, and calculated a correlation matrix among all of them. Then we retained the variables that had the highest correlation with the response variable and, at the same time, a correlation below 0.8 with the rest of the retained climatic variables. On the second step, we compared all the possible models including the preselected variables by means of their partial Akaike weighting (Burnham & Anderson 2002; Diniz-Filho, Rangel & Bini 2008). In order to account for uncertainty in the model selection, we also calculated the importance of the variables, computed as the sum of the relative evidence weights of all the models in which the variable appeared (Mazancourt & Calcagno 2010). We selected the variables that were included in at least 80% of the best 100 models, ranked on the basis of their AIC values (Mazancourt & Calcagno 2010). After the selection of predictors was done, we checked the residuals of the models in order to detect heteroscedasticity, departures from normality and to identify outliers. This procedure was repeated for the general data, and also for the subsets of data defined by the modules found in the network analyses. Since some of the modules were represented by a small number of forests (*ca.* 10), we limited the number of final variables in the model so that there was always at least five data points per variable. Finally, to evaluate the independent contribution of environment and commonness we conducted partial regressions (Legendre & Legendre 1998). To check whether there is any effect of sample size we performed additional regression analyses for the largest modules, evaluating the results on 100 random subsamples with 12 forests per subsample.

Between-forest dissimilarity

To assess the importance of the environmental variables and the changes of commonness on species composition over the landscape, we used a Generalized Dissimilarity Model approach (as implemented in Ferrier *et al.* (2007). This method is an extension of matrix regression that can accommodate curvilinear relationships between compositional variations –measured by the Sorensen dissimilarity index– and both environmental distance and turnover rate Ferrier *et al.* 2007). To avoid an eventual spurious inflation of the influence of climatic variables and multicollinearity problems we performed an NMDS ordination with the 19 bioclimatic variables and extracted the two first axes. Then, we included the rest of the environmental variables, spatial distance and the two axis in the GDM model, and performed a selection procedure following Ferrier *et al.* (2007). To do so, we first deleted the variables that had a very small contribution (sum of the coefficients = 0) and then removed the next variable with the smallest contribution and checked whether the simplified model was significantly worse than the model including that variable. After the selection, we evaluated the relative weight of each variable group (climate, distance and commonness) by means of variation partitioning (Legendre & Legendre 1998).

7.3 Results

Biogeographic modules

The networks of epiphytic bryophyte communities were significantly modular (i.e. it had a modularity index significantly higher than random networks, see Appendix E.2, supplementary material) at all the analyzed scales (Mi forest binary=0.26, p=0.01; Mi tree binary=0.37 p=0.01; Mi forest abundance= 0.37, p=0.01; Mi tree abundance=0.62, p=0.01). The number of modules varied across measures and scales (Fig. 7.1b). For the binary measures at forest and tree scales the analyses recognized 4 and 7 modules respectively (Fig. 7.1 c and d), and for the abundance data at forest and tree scales 7 and 13 modules were recognized (Fig. E2, supplementary materia). For binary data at forest scale, three of the modules showed a clear geographic pattern in the study area (Fig. 7.1 c): module 1 was mostly located in the NW, within the region under Atlantic climate; module 2 mostly occurred in mountainous areas under soft Mediterranean climate; and module 3 was mainly distributed throughout basal areas with more typical Mediterranean climate. In contrast, module 4 showed no clear geographic pattern, since the forests pertaining

to this module were scattered across the territory and showed low inter-modular connectivity (small sized circles in (Fig. 7.1c). Results for binary data at tree scale (Fig. 7.1d) were similar, four of the seven modules were dominant in forests across a particular geographic zone: module A was mostly constrained to the NW of the study area; module B was mainly distributed throughout the mountainous areas of the Mediterranean region in the study area; module E was related to basal areas under Mediterranean climate; and module F was clumped in the eastern mountains (Iberian System) of the study area. Besides, two of the seven modules showed a dominant but restricted distribution. That is, the trees pertaining to these modules were dominant only in a few forests, while in the rest of their distribution they appeared co-occurring with trees from other modules: module C was dominant only in one forest in the north of the study area, and also appeared scattered within forests dominated by module B trees; similarly module D trees were dominant only in two forests in the western part of the study area, and also appeared scattered in lowland forests that were mostly dominated by module E trees. Finally, module G trees were not dominant in any forest but appeared scattered throughout the territory.

The correspondence between the modules found at each of the two scales was strong (Fig. 7.1b). At the tree scale most of the trees pertaining to module A belong to the forest scale module 1. Similarly, module B trees were strongly related to module 2 at forest scale, although module C trees also had a relevant participation in module 2 (Fig. 7.1b). Also, the trees from modules D, E and F were mostly related to module 3 at forest scale. Finally, module G trees were scattered through all the modules at forest scale. Besides, pairwise similarity values of species co-occurrence into modules (measured by Schoener's index, see Appendix E2, supplementary material) showed a high correlation between the two scales (Spearman rho= 0.79, $p<0.01$).

The results for the analyses based on abundance data followed the same general scheme as binary data (Fig. E2, supplementary material), although more modules were detected at both scales and a higher number of modules showed scattered distributions without clear geographic patterns. In general, most of the modules showed a clear geographic pattern, and across scale coherence of modules was also high (although less strong than in the binary data analyses). Alike binary data, Schoener's co-occurrence index showed a high correlation between scales (Spearman rho=0.64, $p <0.01$).

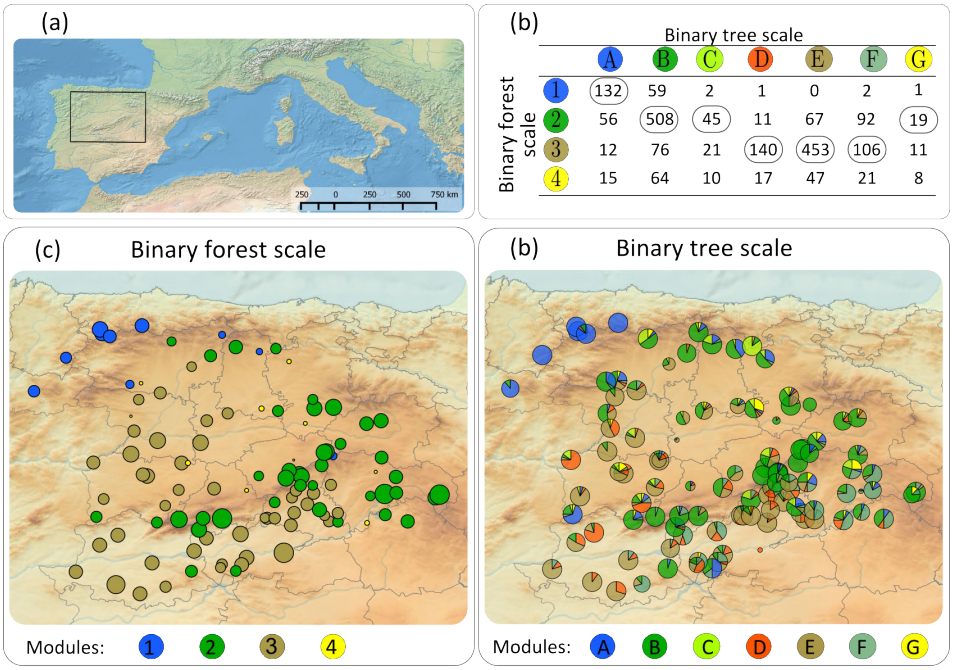

Figure 7.1: Summary of the results of the network analyses for presence-absence binary data. (a) The black quadrat represents the area covered in the study. (b) Table relating modules in the network at tree (columns) *vs.* forest (rows) scales. Data in the body of the table are the number of trees in each category, for example, module 1 includes 132 trees in module A, 59 trees in module B and so on. For each module at the tree scale (column), the highest figure is circled. (c) Distribution of modules at the forest scale. Circle colors depict the module to which the forest belongs. Circle size indicates the degree of participation of the forest in its module, that is, the density of links that the forest has within the module in relation to the density of links outside the module. (d) Distribution of the modules at the tree scale. Each pie represents a forest while the sectors of the pie indicate the percentage of trees belonging to each module in that forest. Pie size is related to the percentage of trees colonized by bryophytes in that forest

Species roles

Six different roles are represented in the binary networks at the tree and forest scales (Fig. 7.2b; Table E1 ,supplementary material). Both at forest and tree scales, the most frequent roles were exclusive and rare (23 species), characteristic (21 species), and occasional but preferential (20 species). The distribution of species roles across modules was largely uneven at both scales. At the forest scale most species showed a clear preference for one module, and only one species was classified as ubiquitous: *Hedwigia ciliata* from module 3, that was in fact very close to the limit

with widespread but indicator species. Module 1 was mostly composed of exclusive and rare (11) and exclusive and common (9) species. In module 2 there were no exclusive and common species, but the other roles were well represented, being widespread indicators the most frequent role (7 species), followed by occasional but preferential, characteristic and exclusive and rare species (6, 5 and 4 species respectively). Module 3 was dominated by characteristic species (14), followed by occasional but preferential role (6). Finally, module 4 was mostly composed of exclusive and rare role (6 species) while the remaining roles had less than 3 species. In the case of the binary network at tree scale, module A was mainly composed of exclusive and common (11) and exclusive and rare (9) species. Modules D and E had a similar distribution of roles, where characteristic species were predominant (9 and 8 species respectively), with occasional but preferential, and exclusive and rare species also represented (*ca.* 4 species). Modules B, C and F were characterized by a smaller number of species and the importance of widespread but indicator species. Finally, in module G all the roles were more or less equally represented. For abundance data the outcome (Table E1, supplementary material) was qualitatively similar to the binary networks, the most important difference being that, in general, exclusive and rare and, especially, exclusive and common species are less frequent. Complete data on species roles can be found on Table E1, supplementary material.

Environmental and biotic constraints

Within forests

β_{sim} retained most of the variability (mean β_{sim} percent of β_{sor} 82.1%, cf boxplot in Fig. E3 (supplementary material), so the analyses of environmental filters are based exclusively on the turnover component of beta diversity. The selection procedure shows that 10 variables are relevant for explaining within-forest beta diversity across scales (Table 7.1 see also Table E2, supplementary material). The overall model explained 56.4% of variability and included 5 variables: commonness, slope, forest type, bark roughness and leaf area index. All environmental variables together explained 15.1% of variability while commonness explained 38.6% of variability, being the joint variability very low.

The analyses per module showed large variations in the selected variables and their independent contribution for explaining beta diversity (Table 7.1, see also Table E2, supplementary material). Commonness was the only variable selected

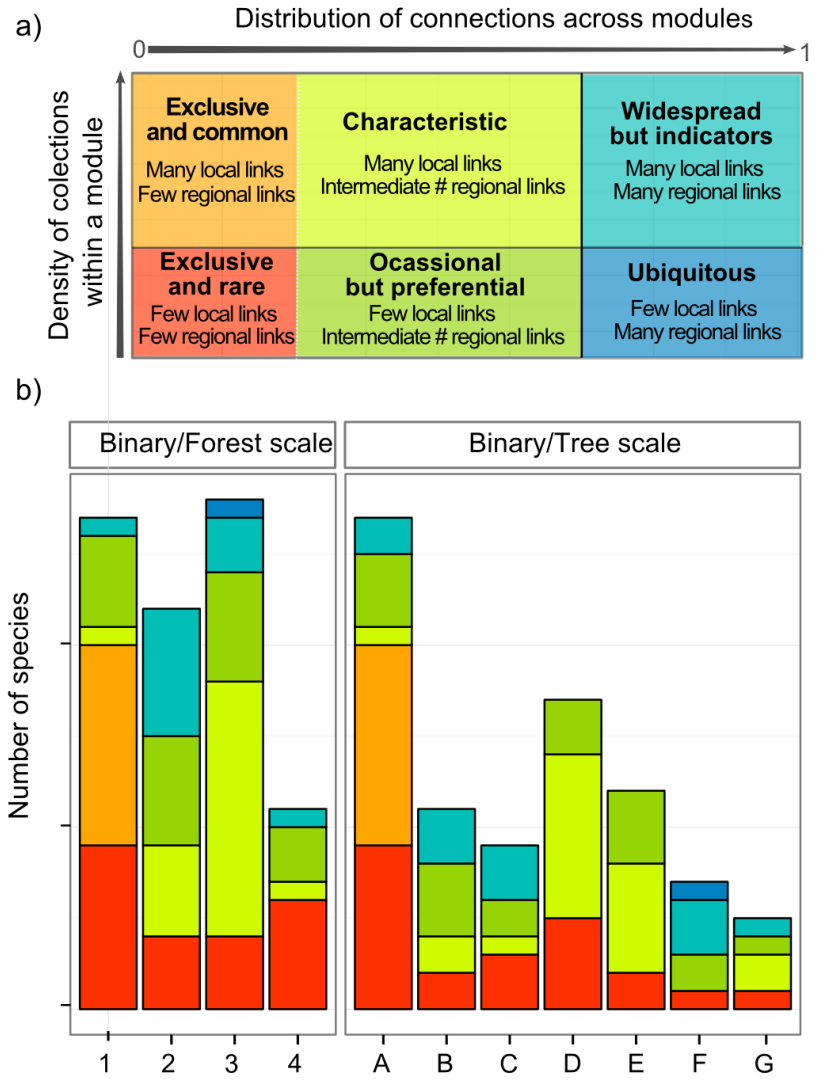

Figure 7.2: a) Schematic representation of the six species roles found in the analyzed communities. Separations among roles were defined after (Guimerà & Amaral 2005; Carstensen *et al.* 2013), see text for detailed explanations. b)Distribution of species roles across modules. Ub: Ubiquitous; Wil: Widespread but indicators; Ocp: Occasional but preferential; Ch: Characteristic; ExC: Exclusive and common; ExR: Exclusive and rare

in modules 1 and 4. In module 2 (Table E2, supplementary material), the selected variables included were commonness, mean diurnal temperature range, slope, forest type, and bark roughness. In module 3 (Table E2, supplementary material), the selected variables were commonness, precipitation of warmest quarter,

Table 7.1: Results of the variance partitioning of the regression of within forest beta-diversity

	All modules	Module 1	Module 2	Module 3	Module 4
Total	56.4	61.9	61.4	79.1	94.5
Commonness	38.6	61.9	11.9	27.9	94.5
Environment	15.1		52.8	31.7	
Joint	2.6		-3.3	19.3	

precipitation of the driest month, precipitation of the coldest quarter, slope and canopy depth. In module 2 (Table 7.1), environmental variables explained 52.8% of the variability, while commonness explained a low proportion of the variability (12%); joint variation was relatively small and negative. In module 3 (Table 7.1), environmental variables explained 32% of the variability while commonness explained 28% of the variability for module 3; the joint variability was relatively high (19.3%). We evaluated the consistency of these patterns for the two largest modules (2 and 3) using random subsamples, and results were similar to those obtained considering the whole set of forests (not shown).

7.3.0.3 **Between forests**

The most important factors explaining beta-diversity between forests (Table 7.2, Table E4) were commonness, climate, slope, two forest structure factors (canopy cover and forest diameter), the two heterogeneity variables (measuring habitat and micro-scale heterogeneity) and three of the descriptors of the micro-environment (bark roughness, canopy depth and leaf area index). The model including all the data points explained 49.4% of deviance. The independent effect of the environmental variables explained 27.3% of deviance while the independent effect of commonness alone explained 17.9 % of deviance; geographic distance and the joint effects of all variables were unimportant. The results per module showed that total explained deviance was variable across modules (from 46.0% in module 3 to 93.2% in module 1). Environmental variables (Table 7.2) were the most important for explaining beta diversity in all modules except 4, where commonness was the preeminent variable. Distance alone showed a very small independent contribution in all modules.

Table 7.2: Percentage of deviance of between forest beta-diversity explained by each group of variables

	All modules	**Module 1**	**Module 2**	**Module 3**	**Module 4**
Total	49.4	93.2	46.0	49.7	60.9
Commonness	17.9	2.64	2.22	9.5	57.7
Environment	27.3	16.2	23.7	29.1	24.5
Distance	1.7	0.28	3.8	1.8	0.02
Joint	2.4	74.1	16.22	9.3	6.9

7.4 Discussion

The geographical structure of epiphytic bryophyte assemblages identified by the network analyses is highly congruent across scales (Fig. 7.1, Fig. E2, supplementary material). This is despite the variable number of modules (from 4 to 13) distinguished by the analyses developed at different scales and type of data. Although forest assemblages are frequently the result of the mix of several modules at the tree scale and the number of modules is larger at tree scale than at forest scale, both the spatial distribution of the modules and the species co-occurrence patterns are strongly consistent across scales. While tree scale partitions seem to reflect subtle variations in floristic tendencies, in general terms they are also strongly coherent with the modules found at forest scale.

Despite their overall congruence, the modules showed different levels of definition and degree of coherence across scales. The northwestern module (modules 1 and A in (Fig. 7.1) is the most clearly defined since it remains consistent across scales and types of data (cf. Fig. 7.1 and Fig. E2, supplementary material). This module is characterized by a high number of exclusive species (Fig. 7.2a) such as *Dicranum scoparium, Frullania microphylla* or *Ulota bruchii* (Table E1, supplementary material). Forests of this module fall within the so called Atlantic region as defined in a previous regionalization based on bryophyte distribution at European extent (Mateo *et al.* 2013). The rest of the modules are less well-defined, and so modules 2 and 3 at the forest scale are defined by non-exclusive species –such as widespread but indicator species like *Orthotrichum acuminatum* and *O. affine* in the case of module 2, or *O. comosum* and *Syntrichia virescens* on module 3–, and appear subdivided into smaller modules when analyzed at tree scale or taking into account species abundances (cf. (Fig. 7.1 and Fig. E2, supplementary material). In the opposite side is module 4 which is poorly defined: although characterized by a number of exclusive and rare species, these are facultative epiphytes that only occa-

sionally colonize tree trunks (Mazimpaka & Lara 1995) , such as *Tortula subulata* or *Tortella inflexa*.

In short, these results seem to reflect the relatively steep transition between the Atlantic and Mediterranean regions as well as the gradual nature of the transition between the different types of communities within the Mediterranean. The Atlantic region was already present in one of the earliest regionalizations of Europe based on vascular plants (Braun-Blanquet 1923) and has been identified as a distinct region in most phytogeographical divisions of the Iberian Peninsula since then (Bolós 1985; Takhtajan 1986; Rivas-Martínez & Loidi 1999; but see Heikinheimo *et al.* 2012). Although the precise limits of this region are controversial, the consistency in its definition across biotic regionalizations suggests that the forces that gave rise to the differentiation of the Atlantic and Mediterranean floras have had a similar effect on a large set of plant groups, such as vascular plants and bryophytes. Furthermore, the gradual nature of transitions encountered within the communities thriving in the Mediterranean area is consistent with the difficulties found by other authors in the differentiation of distinct areas within the Mediterranean region (see review in Rodríguez Guitián & Ramil-Rego 2012).

Interestingly, the result at forest scale based on binary data has important similarities with the one proposed by Bolós (1985), with module 2 being related to the Submediterranean province and module 3 being enclosed within the limits of the Mediterranean region *sensu* Bolós (1985). Similarly, Mateo *et al.* (2013) showed that large-scale vegetation patterns and bryophyte distributions show a remarkably congruent pattern when analyzed by analogous methodologies. Taking into account the disparity of methods used in the regionalizations proposed, it seems that in spite of the differences in biotic characteristics and dispersal traits, the differentiation of regional floras among vascular plants and bryophytes have responded in a similar way to major environmental and historical factors (Schofield 1992).

Our results show that epiphytic bryophyte communities are highly heterogeneous within forests. The high turnover across trees and the lack of nested variations imply that multiple more or less stable combinations of species are occurring simultaneously within forests. This pattern contrasts with the finding of a common pattern of modules across scales suggesting that species that colonize a tree tend to be associated to a common regional pool. This supports former evidence that epiphytic bryophytes are structured in a top-down hierarchical fashion (Medina *et al.* 2014), consistent with the scaling scheme proposed by Guisan & Rahbek (2011) in which regional factors have a strong influence on structuring of local communities.

The analysis of the strength of environmental filters and abundance-based processes reveals that both environment and commonness have a large influence on beta diversity within a forest. We detected notable differences in the relative importance of environmental filters and commonness across modules. In fact, two distinct types of patterns can be identified in the study area; while commonness was predominant in modules 1 and 4, this factor shares influence with environmental conditions in modules 2 and 3. This indicates that, besides –or because of– occurring at different environmental conditions and showing important differences in essential attributes (such as the regional pool, the linkage pattern and species roles), the different modules show different balances in the processes structuring beta diversity (Myers *et al.* 2013). These differences point to a modulation by regional-scale factors of the forces structuring beta diversity at local scales (Pärtel 2002; Harrison & Cornell 2008), reinforcing the idea that regional processes have a deep influence on local diversity processes.

The negative relationship between commonness and beta diversity indicates that the forests with larger populations of common species –and smaller populations of rare species– will show relatively homogeneous tree communities. Note that commonness offers a synthetic measure of the dominance structure in the community (Arellano *et al.* 2014) where high values of commonness indicate an overrepresentation of common over uncommon species within the forest. Hence, the balance between commonness and the effect of environmental filters can help assessing the importance of neutral processes. Given the large dispersal ability of bryophytes, locally common species –those with high local abundance and frequency– would be the ones able to monopolize most of the trunks available in the forest (following De Meester *et al.* 2002). Such a monopolization could occur through either environmental filtering or neutral processes (i.e. ecological drift, Hubbell 2001). Under a niche-deterministic scenario there would be a higher degree of conspecific aggregation (i.e. high commonness) around certain environmental values (i.e. the same species tend to occupy similar environments), thereby linking commonness, community composition and beta diversity to environmental filtering. Conversely, if such a conspecific aggregation is independent of environment –and thus has unique effects on beta diversity patterns– these effects can be related to pure abundance-based processes (i.e immigration, extinction and occupancy dynamics). Hence, we argue that if commonness has an effect upon beta diversity that is independent of environment, then this effect can be interpreted as a sign of the importance of neutral processes. Interestingly, commonness shows important effects on all modules suggesting that neutral abundance-based processes

are relevant for structuring bryophyte communities, at least at small scales. Besides commonness, environmental filtering also showed a relevant contribution to species replacement within forests. In particular, in the forests pertaining to modules 2 and 3 beta diversity among trees was related to forest type and climate respectively (Table E2, supplementary material).

The relative importance of environmental filters and commonness is consistent with the hypothesis of environmental harshness (Chase 2007, 2010) as outlined in objective 2. This hypothesis states that in harsher conditions the size of the effective pool colonizing the trees (and ultimately the number of species) is limited by environmental conditions favouring an over-representation of the species adapted to the local conditions, thereby leading to higher commonness values associated to certain environmental conditions. Confirming this hypothesis, module 1 is at the same time showing the weakest relationship between species replacement and environmental variables, and the environmental conditions most favourable for bryophytes, with significantly higher precipitation of the driest month and of the coldest quarter and milder temperatures during the wettest quarter (data not shown). On the contrary, modules 2 and 3 show relatively strong relationships with environment, while occurring in forests with harsher conditions. Module 4 represents an exception to this rule since it is embedded within the area under relatively harsh conditions and yet shows a strong influence of commonness without a strong contribution of environmental filters. However, the significance of this module is difficult to interpret since the module shows no clear biogeographic pattern, is very poorly defined and is inconsistent across scales and measure types.

On the whole, our results allow concluding that within-forest variations in bryophyte communities are close to neutral in some of the modules. Further, there is no apparent effect of niche-driven assembly processes on beta diversity at the smallest scale in the Atlantic region. These results are specific of this group and study area. However, they provide strong support for the balance between niche and neutral processes as a major determinant of beta-diversity patterns, being neutral processes more important in the environmentally more favorable regions, where the effects of environmental filtering are weaker.

In contrast, the compositional dissimilarity between forests is mostly explained by environmental differences. Neither commonness nor spatial distance between forests have strong pure effects on beta diversity patterns at this scale. The lack of effect of spatial distance might be related to the high dispersal ability of bryophytes, and suggests that there are no major barriers to dispersal for this group within the study area. Niche-deterministic factors are more important at larger

scales (Legendre *et al.* 2009; Shipley *et al.* 2011); while small populations are largely affected by stochastic fluctuations, mean success per species increases as population size increases (Shipley *et al.* 2011).

7.5 Concluding remarks

By describing the patterns of species co-occurrence as a bipartite network we have been able to identify both chorotypes and the groups of sites where they occur, allowing a meaningful description of both the main biotic transitions within the study area and the small-scale replacement between highly similar communities. Such a comprehensive description allowed us to identify the structuring of epiphytic bryophyte communities as a by-product of the balance between niche-related and neutral processes. The balance between both processes changes throughout space, being neutral stochastic effects larger in the most favourable regions. The impact of these stochastic processes diminishes as scale increases, being minimal for the bryophytes we study in a gradient of *ca.* 400 km. Rather than the output of contradictory bodies of theory, neutral and niche processes are intrinsic parts of all community assembly processes, that coexist and intertwine in across scales in a structured way, which in turn depends on the spatial dynamics of each group, the environmental variability of the region and the species present in the pool of potential colonizers.

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CHAPTER

8

Discusión general

En los capítulos anteriores se ha analizado la diversidad de los briófitos epífitos en la porción interior del centro y norte peninsular desde diferentes puntos de vista, intentando contextualizar los resultados dentro de un marco teórico común, lo que ha permitido identificar los factores que más influyen en la explicación de dichos patrones. En este capítulo se discuten brevemente los resultados principales del trabajo, atendiendo a los diferentes aspectos trasversales que se han tratado en varios de los capítulos anteriores. Se abordará primero la complejidad de los patrones de diversidad para comentar después el valor de los procesos sistemáticos de selección de áreas y la integración del conocimiento previo en los diseños de muestreo. Finalmente, se analizan los principales factores que explican la diversidad de briófitos epífitos en el área de estudio y las conclusiones más importantes sobre el escalamiento de los procesos, para terminar discutiendo la importancia de estos resultados en un marco más amplio y la posible proyección futura de los mismos.

Comprensión de los patrones de diversidad: entendiendo un fenómeno complejo

El marco conceptual sobre el que descansa esta tesis doctoral propone estudiar la diversidad como resultado de un conjunto de factores interrelacionados que incluyen procesos evolutivos, dispersivos, filtros ambientales e interacciones bióticas (Rajaniemi 2003; Guisan & Rahbek 2011). La idea que subyace a este marco conceptual es que no es posible estudiar la complejidad de los sistemas biológicos analizando solamente sus partes (Grace 2006; Parrott & Meyer 2012). Desde el punto de vista metodológico, abordar un análisis integrativo como el expuesto más arriba supone un reto importante. Por un lado, diseñar un muestreo adecuado –que recoja información sistemática para todos los factores implicados– es una cuestión difícil. El compromiso entre los recursos humanos y económicos disponibles y la necesidad de realizar una serie de medidas a pequeña escala a través de un territorio amplio ha supuesto unos condicionantes importantes. El objetivo de medir una amplia gama de variables a pequeña escala se ha podido conseguir, en gran medida,

gracias a la información previa sobre briófitos epífitos acumulada a lo largo de los últimos 25 años por el equipo de trabajo en el que se ha desarrollado esta tesis (Lara 1993; Albertos *et al.* 2001; Cortés 2005; Medina *et al.* 2010). Sin embargo, las limitaciones naturales en el esfuerzo de muestreo y los recursos han impedido incluir algunos aspectos que merecerían un estudio en profundidad y que se espera poder abarcar en un futuro. Entre estos destacan el efecto sobre los resultados de ampliar el gradiente en condiciones microclimáticas o el análisis espacialmente explícito de los patrones a la menor de las escalas. Por otro lado, el análisis matemático de modelos que incluyen un número importante de variables de naturaleza muy diferente, medidas a resoluciones distintas y estructuradas de forma anidada, ha supuesto un reto metodológico que ha impuesto la exploración de técnicas novedosas, a la vez que complejas. Un buen ejemplo de ello es la integración de modelos mixtos en los modelos de ecuaciones estructurales, lo que ha permitido descubrir los efectos de algunos factores a través de las escalas (Capítulo 6), o la incorporación de análisis de redes de co-ocurrencia de especies para delimitar comunidades, de forma que se consideran simultáneamente dos niveles: los lugares con mayor número de especies que tienden a ocurrir juntas, y las especies que más co-ocurren entre sí (Capítulo 7). Sin embargo, estas metodologías, ventajosas en otros aspectos, tienen la desventaja de incrementar la complejidad técnica del trabajo, lo que puede dificultar su accesibilidad. Además, en contraste con lo que sucede con técnicas clásicas −como la regresión lineal múltiple, por poner un ejemplo− sobre las que existe un amplio conocimiento en lo relativo a la robustez y la respuesta frente a los sesgos en los datos, estos aspectos son menos conocidos en algunas de las nuevas técnicas empleadas en este estudio.

Muestreo de briófitos epífitos en el entorno mediterráneo

Una de las aportaciones interesantes de esta tesis doctoral consiste en haber ampliado sustancialmente el conocimiento de la distribución de los briófitos ibéricos, completando los huecos en el conocimiento de las distribuciones de un buen número de especies en el área de estudio. Disponer de datos de calidad, que describan de forma precisa los patrones de biodiversidad, es una cuestión de gran importancia (Hortal, Lobo & Jiménez-Valverde 2007), tanto si el objetivo es diseñar estrategias de conservación, como si es el estudio de los patrones de diversidad y los procesos que los originan. En el caso de los análisis de patrones de diversidad, es bien conocido que los sesgos en la adquisición de datos pueden comprometer la fiabilidad de los resultados (Hortal *et al.* 2007). Precisamente, los sesgos que son habituales

en la descripción de las distribuciones de los grupos taxonómicos mejor conocidos están también presentes en el estado de conocimiento de los briófitos ibéricos. Como suele ser habitual en los organismos de pequeño tamaño (Whittaker *et al.* 2005; von Konrat *et al.* 2010; Geffert *et al.* 2013; Fontaneto & Hortal 2013), el conocimiento acumulado es limitado (Lara *et al.* 2005). Además, los datos de ocurrencia de especies están condicionados por el sesgo espacial en el esfuerzo de muestreo (Aranda *et al.* 2010; Medina NG *et al.*, 2013). Así, las zonas montanas más singulares o los entornos de las residencias de los especialistas han sido herborizados con mayor intensidad que las zonas basales de los diferentes territorios. Por esta razón en el presente trabajo se ha enfatizado la importancia de generar bases de datos representativas de los gradientes ambientales y geográficos que se pretende estudiar, poniendo especial cuidado en la selección de puntos de muestreo y en el diseño de la toma de datos en el campo.

La consecución de una base de datos precisa y de calidad requiere tres pasos (Aranda *et al.* 2015): 1) la recopilación de la información previa, 2) la planificación de un diseño de muestreo que complete los huecos en el conocimiento, y 3) la evaluación de los resultados del muestreo. En relación al primer paso, en el caso presente se contaba con una serie de muestreos sistemáticos realizados a lo largo de las últimas décadas en áreas localizadas dentro de la zona de estudio (Lara 1993; Albertos *et al.* 2001; Cortés 2005). Esto ha facilitado enormemente el diseño de una estrategia de muestreo eficiente, permitiendo de esta manera profundizar en aspectos centrales de este trabajo, como son la medición de factores ambientales a diferentes escalas. En cuanto al diseño de una estrategia de selección dirigida a completar los huecoscolmar las lagunas de conocimiento, la cuestión se ha solventado mediante el uso de un protocolo de selección que tiene en cuenta tanto la información previa como los gradientes ambientales y geográficos a cubrir.

Además, en relación con la evaluación de los resultados, en una etapa intermedia del proceso de muestreo se realizó una comprobación en la que se estableció cuál era el nivel de esfuerzo de muestreo necesario para representar de forma adecuada la diversidad de la zona de estudio. Esto se consiguió mediante la modelización de la riqueza de especies esperada utilizando curvas de acumulación (Hortal, Borges & Gaspar 2006) e índices que dieran una idea del porcentaje de riqueza que se podía capturar a distintos niveles de esfuerzo de muestreo (Chao *et al.* 2009). Teniendo en cuenta las limitaciones de tiempo y recursos, en total se seleccionó aquel esfuerzo de muestreo que recogiera entre un 81 % (melojares) y un 99 % (quejigares) de la riqueza máxima estimada. Pero, además de evaluar la calidad de los muestreos en relación a la riqueza capturada, también se evaluó la

representatividad ambiental y geográfica de los bosques seleccionados. En total, el esfuerzo de muestreo seleccionado permitió alcanzar una representatividad del 98 % de la variabilidad ambiental y geográfica. Sin embargo, si consideramos tan sólo la variabilidad ambiental, la que fue posible recoger en el caso de los encinares no superó el 50 % de la variabilidad total de estos bosques en el territorio. Esto se debe al bajo estado de conservación de los encinares en el área, ya que no todas las combinaciones de condiciones ambientales contienen encinares bien conservados (Costa, Morla & Sainz 2005). A su vez, la evaluación del esfuerzo de muestreo necesario para representar de forma adecuada la diversidad dentro de cada uno de los bosques ha sido posible gracias a que se conocía con anterioridad el número de muestras necesarias para representar de forma adecuada la diversidad de briófitos epífitos en los bosques de la península ibérica (Lara 1993; Albertos *et al.* 2001; Garcia 2006). Esto, unido al uso de curvas de acumulación, permite caracterizar de manera explícita el compromiso entre alcanzar mayores niveles de conocimiento y dedicar esfuerzo de muestreo adicional. Este tipo de estrategia, basada en priorizar la calidad de los datos y comprobar de forma explícita la representatividad, es poco habitual debido, sobre todo, a los recursos (humanos y económicos) que es necesario invertir para diseñar y evaluar de forma exhaustiva los diseños de muestreo (Aranda *et al.* 2015). Sin embargo, obviar este paso puede derivar en la realización de un sobreesfuerzo importante y eventualmente innecesario (Aranda *et al.* 2015) o en una representación pobre de los gradientes que se quieren analizar.

El éxito de la estrategia utilizada ha quedado reflejado en las numerosas aportaciones al conocimiento de la distribución en la Península Ibérica. Destaca el elevado número de novedades provinciales encontradas (más de 70), sobre todo porque algunas de las especies que acumulan más localidades novedosas, como por ejemplo *Orthotrichum acuminatum,* son especies comunes y relativamente fáciles de identificar. Además, tal y como se había previsto, se ha detectado un importante sesgo espacial en el conocimiento de la brioflora epifita, de forma que las provincias ubicadas en las zonas menos montañosas de las dos mesetas acumulan un número significativamente mayor de novedades, lo que da una idea de los bajos niveles de esfuerzo de muestreo invertidos en estas regiones. Este resultado deja patente la necesidad de recopilar datos en regiones que *a priori* son consideradas poco interesantes, como son las áreas con mosaicos de bosque y paisaje agrario de las mesetas ibéricas. Es muy posible que la situación del conocimiento encontrada para los briófitos epífitos sea similar a la que tienen los musgos y hepáticas que crecen en otros sustratos. Por lo que, si extrapolamos los resultados encontrados en este trabajo al conjunto de los briófitos en la península ibérica, llegaremos a la

conclusión de que es necesario diseñar una estrategia de muestreo a escala ibérica que persiga el objetivo de describir las distribuciones de las especies. Un diseño de muestreo basado en el protocolo que presentamos en el Capítulo 3 permitiría realizar evaluaciones sobre el éxito de la estrategia de muestreo cada vez que hubiera disponibles recursos para recolectar datos, permitiendo adaptar el progreso del trabajo a los recursos disponibles. Pero para ello, el primer paso sería realizar una evaluación del estado inicial y detectar los huecos en el conocimiento más importantes, lo que permitiría posteriormente diseñar unos muestreos dirigidos a minimizar la inversión de recursos, maximizando con ello la capacidad de los resultados para describir las variaciones en la diversidad de briófitos a todo lo largo y ancho de la Península Ibérica.

Factores determinantes de la diversidad y la estructura de las comunidades de briófitos epífitos a través de las escalas

En varios de los trabajos que conforman esta memoria doctoral se ha constatado la importancia del *pool* de especies (el conjunto de especies disponibles a una escala determinada) en la estructuración de las comunidades. Así, se ha comprobado que el tamaño del *pool* tiene un efecto trascendental sobre la riqueza. Además, cuando se caracteriza en detalle la composición florística se puede observar que en los bosques pueden convivir varias combinaciones de especies (comunidades regionales *sensu* Ricklefs 2011) de forma simultánea, generando una importante variación en la composición entre árboles. El establecimiento de una u otra comunidad regional en los árboles de un bosque determinado no parece estar íntimamente vinculado con las condiciones ambientales, o al menos no de manera directa. Además, las especies que cohabitan a escala de árbol tienden a hacerlo también en el conjunto del área de estudio, conformando un patrón en el que el efecto del *pool* regional es perceptible de forma muy notable a escala de árbol. Los resultados aquí expuestos se suman a la creciente evidencia de que los factores regionales −entendidos como cualquier proceso que sucede más allá de los límites de la propia comunidad− son importantes para estructurar las comunidades (Ricklefs 1987, 2007). El que la confirmación proceda en este caso de briófitos es muy relevante, pues se trata de un grupo de organismos con una alta capacidad dispersiva, donde el movimiento de individuos entre poblaciones favorecería, en teoría, el establecimiento de comunidades en equilibrio con las condiciones locales, minimizando el efecto de posibles limitaciones a la dispersión y en consecuencia la influencia de factores regionales (Schluter & Ricklefs 1993).

El efecto de los filtros ambientales se produce cuando factores bióticos o abióticos limitan la presencia y/o abundancia de una especie en una comunidad y dan como consecuencia una ordenación predecible −y en ese sentido determinista− de la diversidad (Keddy 1992). Como consecuencia del efecto de los filtros ambientales, las distintas medidas de diversidad se correlacionarán bien con los factores ambientales. A pesar de que la teoría neutra ha puesto en duda la necesidad de invocar factores deterministas para explicar algunos patrones emergentes de la diversidad (Hubbell 2001; Condit *et al.* 2002; Volkov *et al.* 2007), también es cierto que la importancia de la limitación que imponen los filtros ambientales a la diversidad se ha demostrado en multitud de organismos y a distintas escalas (ver, por ejemplo Chase 2011). Aquí, para los briófitos epífitos, se ha constatado que la variación de la diversidad entre bosques −tanto en riqueza como en composición específica− está vinculada principalmente a los gradientes ambientales a lo largo del territorio. Esto queda reflejado en la diferenciación biogeográfica entre las regiones Mediterránea y Atlántica (Fig. 7.1, así como en la importancia de los factores ambientales sobre la riqueza a escala de bosque (Figs. 2.6 y 6.3) y sobre la beta diversidad entre bosques (Tabla 7.2). Así, las dos regiones biogeográficas que afectan al área de estudio están caracterizadas por conjuntos diferentes de especies, en buena medida pertenecientes a linajes bien separados. En el módulo asociado a la Región Atlántica, destacan los musgos pleurocárpicos y algunos géneros de hepáticas. Por contra, en los módulos asociados a la Región Mediterránea las especies del género *Orthotrichum* son con mucha frecuencia dominantes. Además, un buen número de las especies que habitan los bosques mediterráneos del área de estudio presentan aparentes adaptaciones fisiológicas y morfológicas a los ambientes secos que colonizan, como por ejemplo el desarrollo de filidios con pelos hialinos en el caso de *Orthotrichum diaphanum* o *Syntrichia laevipila* o el hábito almohadillado de muy pequeño porte, característico de *Orthotrichum schimperi* y *O. tenellum*, entre muchos otros. Aunque a lo largo de esta tesis doctoral no se han estudiado de forma directa los procesos evolutivos, sí que se detecta su impronta. Ya que, en último término, su marcada influencia se ve reflejada en la ordenación de las comunidades en función de los filtros ambientales que queda patente tanto en la segregación taxonómica entre las regiones biogeográficas como en las distintas adaptaciones de las especies al ambiente.

A diferencia de lo encontrado a escala de bosque, la diversidad a la menor de las escalas o no ha mostrado una vinculación directa (Fig. 2.3), o ha mostrado una relación débil con los filtros ambientales (Fig. 6.3). Sin embargo, se ha detectado una serie de efectos indirectos que vinculan los filtros ambientales a la diversidad

a pequeña escala. En primer lugar, dado que el efecto del número de especies en un bosque está condicionado por filtros ambientales operando a la meso escala y que a su vez la riqueza a pequeña escala está condicionada por el número de especies de cada bosque, se produce una transmisión del efecto del meso ambiente a la diversidad a escala de árbol. En segundo lugar, debido a que la abundancia está condicionada por filtros ambientales (principalmente características de estructura de bosque y microambiente), en los casos en los que se detecta un efecto de la abundancia sobre la diversidad se produce una transmisión de la influencia del ambiente sobre la diversidad a pequeña escala. Así, aunque no hayamos encontrado una relación directa o íntima entre los filtros ambientales y la diversidad a pequeña escala a nivel general −sí la hay en algunas zonas dentro del área de estudio− ello no implica que la riqueza a escala de árbol sea independiente del ambiente. Muy al contrario, la diversidad a la menor de las escalas está ligada a los filtros ambientales pero de una manera indirecta, de modo que la intensidad del efecto dependerá de la relación de la diversidad con los *pool* de especies a las distintas escalas y con la abundancia. Es posible que si se consideran gradientes micro-ambientales más amplios, como por ejemplo las bases de los árboles o varios ambientes al mismo tiempo, se pueda detectar un efecto directo de los factores microclimáticos sobre la diversidad de briófitos. Pero eso no invalida el hecho de que existe a la vez un efecto indirecto mediado por el tamaño del *pool* de especies y la relación entre diversidad y abundancia. En resumen, el equilibrio entre efecto directo e indirecto –y por lo tanto, la importancia de los factores ambientales sobre la diversidad a la menor de las escalas– dependerá de la extensión del gradiente ambiental y de la fuerza relativa de cada factor en la estructura de relaciones de las que pende la diversidad local.

En cuanto a los procesos dispersivos, no se ha encontrado evidencia de que exista un efecto importante de limitación a la dispersión que condicione las diferencias entre bosques. Aparentemente, el efecto de procesos no deterministas vinculados a la dispersión –relacionados con la neutralidad– en los briófitos epífitos parece ser mayor a la menor de las escalas estudiadas. Son indicios de esta importancia, el efecto relativamente grande del tamaño del *pool* de especies sobre la diversidad a pequeña escala, así como la importancia del efecto independiente del ambiente de la abundancia o de la dominancia sobre la diversidad de las comunidades a pequeña escala. Aunque ni la relación con la abundancia ni el vínculo entre diversidad local y regional son pruebas directas de la importancia de procesos neutros, el hecho de que sus efectos sean detectables con independencia de los factores ambientales

apunta hacia la relevancia de la estructura de tamaños poblacionales sobre la diversidad de las comunidades a pequeña escala. Así, un mayor número de individuos representa un menor riesgo de extinción, mientras que una mayor diversidad regional implica una aportación de propágulos que, en última instancia, favorece la diversidad local. Dado que aquí se ha comprobado que una porción importante de esos efectos es independiente del ambiente, parece que, efectivamente, los procesos neutros son relevantes para explicar los patrones de diversidad a la menor de las escalas. Este resultado sugiere que es necesario incorporar los filtros de dispersión como factores importantes también a pequeña escala, cuando actualmente el marco conceptual en el que se basa esta tesis doctoral (Rajaniemi 2003; Guisan & Rahbek 2011) considera los procesos de dispersión de forma explícita tan sólo a la mayor de las escalas.

Por último, la importancia relativa de los procesos neutros también varía a lo largo del área de estudio. Así, los procesos neutros han resultado ser más importantes en las zonas con unas condiciones climáticas más favorables.

En resumen, tanto los filtros ambientales como los procesos neutros son importantes para explicar los patrones de diversidad encontrados. Los resultados obtenidos apoyan la hipótesis de que los procesos neutros y de nicho representan extremos de un gradiente (Gravel *et al.* 2006; Legendre *et al.* 2009) en el que el balance entre unos procesos y otros depende de la escala del análisis y de los factores regionales. Así, para los briófitos epífitos en el área de estudio, los filtros ambientales son preponderantes a escala de bosque, mientras que los procesos neutros lo son, sobre todo, en las zonas con ambientes más favorables a la menor de las escalas.

Hasta ahora, una buena parte del esfuerzo invertido en el estudio de los efectos de la escala se ha centrado en evaluar la importancia relativa de los factores a una o dos escalas diferentes (Schneider 2001). Sin embargo, a medida que se analizaban los resultados de esta tesis doctoral se ha hecho patente la importancia de incluir los efectos e interacciones a través de las escalas. Esto es, no es suficiente con analizar cada una de las escalas por separado, sino que es necesario considerar los resultados en una escala para interpretar lo que sucede en las demás. La estructura jerárquica de relaciones mostradas en los Capítulos 2 y 6 es un buen indicador de esta necesidad. Pero además, la existencia de relaciones a través de las escalas se ha podido observar en las interacciones entre variables ambientales a pequeña escala y la diversidad a escalas mayores (Fig. 6.3, Tabla E4), de modo que la naturaleza de los efectos de interdependencia va más allá de la relación entre riqueza regional y local.

Líneas de investigación a futuro

Los resultados presentados hasta ahora se basan en datos observacionales y en la inferencia, a partir de ellos, de los procesos más plausibles que subyacen a los patrones detectados. Sin embargo, esta metodología de trabajo tiene la dificultad de tratar de averiguar las causas de manera indirecta, a través de la observación de correlaciones. En consecuencia, existe un cierto grado de incertidumbre con respecto a la interpretación de esas relaciones. Varias líneas de trabajo podrían contribuir a consolidar tanto los resultados encontrados como las interpretaciones sobre los procesos dominantes. Por un lado, sería interesante explorar la relación de la diversidad taxonómica con la diversidad filogenética y la diversidad funcional (Mason & de Bello 2013). Por otro, las interpretaciones realizadas representan en sí mismas un conjunto de hipótesis a analizar desde el punto de vista experimental. Por ejemplo, si es cierto que los procesos neutros son más importantes en zonas con ambientes favorables (de la región Atlántica en nuestro caso), las comunidades de estas zonas, además de una estructura de abundancias relativas con un vínculo débil con las condiciones ambientales (ver resultados de esta tesis doctoral), deberían tener una menor sensibilidad a la manipulación experimental de la abundancia relativa de las demás especies que las comunidades en ambientes más restrictivos (Vellend *et al.* 2014).También podrían analizarse experimentalmente los efectos del orden de colonización y el tamaño del efecto de la estocasticidad sobre la diferenciación de las comunidades en el tiempo, emulando diferentes sucesiones de especies en áreas con condiciones ambientales contrastadas (Vellend *et al.* 2014). Del mismo modo que en otras áreas de la Ecología, no va a ser posible encontrar una prueba definitiva de la importancia de unos procesos frente a otros, de modo que la construcción del conocimiento se debe basar en el propio proceso de investigación (Grace 2006).

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Conclusiones

1 La aplicación de diseños de muestreo basados en protocolos que consideren de forma explícita el conocimiento previo, los objetivos del estudio y los gradientes a representar, es el mejor modo de maximizar la cobertura ambiental y geográfica y optimizar el esfuerzo de muestreo adecuándolo a los objetivos. Esto es especialmente importante para los briófitos ibéricos. Para este grupo se tiene todavía un nivel de conocimiento de las distribuciones de las especies relativamente bajo, que en buena medida viene condicionado por importantes sesgos en el esfuerzo de muestreo. A ello hay que sumarle la extensión y complejidad del territorio ibérico y la escasez de recursos humanos y económicos disponibles. Por lo tanto, para conseguir un conocimiento representativo y de calidad es necesario diseñar una estrategia dirigida a detectar y rellenar los huecos en el conocimiento de forma eficiente.

2 La efectividad del protocolo de muestreo empleado se refleja en la elevada diversidad de briófitos epífitos censados y la acumulación de novedades provinciales. Para alcanzar dichos niveles optimizando el esfuerzo de muestreo es necesario realizar comprobaciones sobre la variabilidad cubierta y el nivel de conocimiento alcanzado. Especialmente debido a que el esfuerzo de muestreo necesario para adquirir un determinado nivel de conocimiento depende de las a contingencias propias de los organismos y del área de estudio el esfuerzo de muestreo necesario para adquirir un determinado nivel de conocimiento puede ser variable.

3 La variación de riqueza y composición de briófitos epífitos entre bosques está condicionada principalmente por las condiciones ambientales. Sin embargo, la diversidad a la menor de las escalas parece estar más vinculada a procesos relacionados con la abundancia y la diversidad regional. Asumiendo que estas relaciones son, en conjunto, indicadores de la importancia de procesos relacionados con la dispersión en la comunidad, se concluye que la escala es, según los resultados obtenidos, uno de los factores que condicionan de forma más notable los cambios en la importancia relativa de los procesos que influyen en la diversidad de los briófitos epifitos. Así, la diversidad depende de factores de nicho a la mayor de las escalas estudiadas pero, a medida que la escala disminuye, los procesos neutros se vuelven más importantes.

4 Las comunidades de briófitos epífitos en el territorio estudiado se caracterizan por estructurarse en un número variable de módulos que presentan una elevada coherencia entre escalas y tipos de medida. En este sentido destaca la Región Atlántica por su estabilidad a través de las escalas y su alto grado de diferenciación florística, que se refleja no solamente en los cambios en la composición de especies sino también en ciertas propiedades de las comunidades, como son la estructura de roles de las especies o la importancia relativa de los filtros ambientales a la menor de las escalas. De este modo, los factores regionales tienen una influencia decisiva tanto en la identidad de las especies que forman las comunidades a pequeña escala como en los procesos que las estructuran.

5 Los datos se ajustan bien, en términos generales, al marco conceptual de relaciones empleado, lo que implica un peso importante de las relaciones jerárquicas de abajo arriba. Esta importancia conlleva a su vez una transmisión de efectos a través de las escalas. Así, los factores ambientales influyen en la riqueza a escala de árbol de forma indirecta, a través del efecto que tienen sobre la diversidad a escala de bosque y la abundancia.

6 Algunas relaciones y procesos detectados conllevan la incorporación de cambios al modelo conceptual empleado. Por un lado, el efecto de los procesos relacionados con la abundancia indica la necesidad de incorporar las dinámicas de ocupación a la menor de las escalas. Por otro, se han encontrado efectos de variables medidas a pequeña escala sobre la diversidad a escalas mayores, de modo que, además de los efectos jerárquicos de arriba abajo, es necesario incorporar efectos de abajo arriba en los marcos conceptuales.

Conclusions

1 The application of a site-selection methodology that explicitly considers previous knowledge, the aims of the study and the gradients of the study area, is the best way to maximize environmental and geographical coverage, as well as to optimize the sampling effort adjusting it to the main objectives of the study. This is especially important for the study of Iberian bryophytes. For this group of organisms, previous knowledge on species distributions is relatively low and has remarkable geographical biases. Extension and complexity of the Iberian territory and the scarcity of human and economic resources are additional handicaps. Thus, to obtain representative and high-quality knowledge on the diversity of bryophytes, it is necessary to design a strategy explicitly aimed at filling in the existing knowledge gaps.

2 The effectiveness in the applied protocol is reflected in the high diversity of recorded bryophytes and the accumulation of provincial novelties. To get such knowledge levels and at the same time optimize the sampling effort, it is necessary to assess the achieved levels of covered variability and attained knowledge. Especially because the environmental variability that is necessary to sample in order to get a certain level of knowledge on biodiversity might be variable due to contingencies in the study area or particularities of the organisms under study.

3 Changes in richness and community composition between forests are mostly related to environmental gradients. However, diversity at the smallest scales seems to be linked to abundance-related processes and species pools. Assuming that these relationships are indicators of the importance of dispersal-related processes in the community, scale appears as a key factor, conditioning the relative importance of the processes involved in the structuring of the diversity of epiphytic bryophytes. Therefore, bryophyte diversity depends on niche related factors at the largest scale, but as scale diminishes, neutral processes become more important.

4 The communities of epiphytic bryophytes in the studied area are structured in a number of variable modules that are highly coherent across scales and measure types. In this sense, the Atlantic region is outstanding because of its stability across scales and high degree of floristic differentiation that is mirrored by the differences in species composition as well as in some community properties, such as the

structure of species roles or the relative importance of the environmental filters at the smallest of the scales. Therefore regional factors have a high relevance on both the identity of the species that form communities and the processes that structure them.

5 Overall, our data match the conceptual framework of hierarchical relationships we applied, which implies that top-down hierarchical relationships have a high specific weight. Interestingly, the importance of the hierarchical relationships entails a transmission of the effects from the largest to the smallest scale. Thus, the environmental factors that influence richness at the forest scale indirectly affect richness at the tree scale through their effect on abundance and species pool.

6 Some of the relationships and processes here assessed entail the need to incorporate changes to the conceptual framework we applied. On the one hand, the importance of the effect of abundance-related processes suggests the need of incorporating occupancy dynamics at the smallest scales into the framework. On the other hand, we have found that some variables at the smallest scales have an effect on the diversity at larger scales. Therefore, besides the top-down effects already included, it is necessary to additionally include bottom-up effects in the macroecological conceptual framework about scaling.

Anexos

Anexo A **Material complementario al Capítulo 2**

Table A1: Summary of the variables considered in the analysis and individual coefficients of the linear regression of environmental variables against overall forest richness, average forest richness and average abundance. Pe: mean monthly rainfall; tc: mean temperature of the hottest month; tf: mean temperature of the coldest month. In the index formula column; P: precipitation, T: temperature and roman numerals indicate month (so that PI is precipitation in January and TXII: mean temperature in December. β : coefficient of the linear regression; r^2: overall goodness of fit. Significance codes: '***' <0.0001 '**'<0.001 '*' <0.01 '.' <0.05 ' ' >0.1. Origin of the variables: precipitation and temperature variables come from SMN (1961-1970), INMG (1971-1990) and INM (1992); bioclimatic indices from Tuhkanen (1980), and altitude from `http://eros.usgs.gov/products/elevation/gtopo30/gtopo30.html`(see main text)

Abbrv.	Variable	Index formula	Overall forest richness		Average forest richness		Average abundance	
			β	r^2	β	r^2	β	r^2
R	Mean anual rainfall		-0.0009***	0.0841	-0.0002	0.0192	-0.0075	0.0054
WR	Mean Winter rainfall (December to February)		-0.0021***	0.0647	-0.0007	0.0230	-0.0062	0.0006
SR	Mean Spring rainfall (March to May)		-0.0031***	0.0938	-0.0010*	0.0295	-0.0333	0.0103
SMR	Mean Summer rainfall (June to August)		-0.0029	0.0119	-0.0004	0.0006	0.0518	0.0036
AR	Mean Autumn rainfall (September to November)		-0.0032***	0.0855	-0.0008	0.0194	-0.0263	0.0056
T	Mean anual temperature		0.0726**	0.0522	0.0322*	0.0331	2.0795**	0.0406
WT	Mean Winter temperature (December to February)		0.0658**	0.0516	0.0282*	0.0305	2.9375***	0.0975
ST	Mean Spring temperature (March to May)		0.0591**	0.0393	0.0232	0.0196	2.0448**	0.0447
SMT	Mean Summer temperature (June to August)		0.0445	0.0156	0.0080	0.0016	0.5550	0.0023
AT	Mean Autumn temperature (September to November)		0.0846**	0.0463	0.0374*	0.0292	3.8167***	0.0894
tmf	Mean minimum temperature of coldest month		0.0595**	0.0454	0.0233	0.0224	2.8257***	0.0972
tMc	Mean maximum temperature of the hottest month		0.0355	0.0145	0.0173	0.0112	-0.0829	0.0001
atr	Mean temperature range	tc-tf	-0.0874**	0.0402	-0.0301	0.0154	-4.7946***	0.1148
Atabs	Absolute temperature range	tmf-tMc	-0.0268	0.0095	-0.0075	0.0024	-2.8088***	0.0992
PCRA	Angot pluviometric coefficient relative of August	365*PVIII/(31*P)	1.5187*	0.0341	0.9118**	0.0397	80.6289***	0.0912
CPRE	Angot pluviometric relative coefficient	Pe/(P)	1.9863*	0.0297	0.8253	0.0166	51.2604	0.0188
G	Summer drought index of Giacobbe	Pe/tMc	-0.0571	0.0176	-0.0171	0.0051	0.5286	0.0014
Imae	Annual aridity of De Martonne	P/T+10	-0.0885	0.0169	-0.0184	0.0024	0.2468	0.0001

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Abbrv.	Variable	Index formula	Overall forest richness		Average forest richness		Average abundance	
IO	Oceanity index of Kerner	(TX-TIV)/at	0.7115	0.0024	0.2935	0.0013	128.85***	0.0733
PH	Summer drought index of Philippis	Pe/tc	-0.0394	0.0154	-0.0121	0.0047	0.0166	0.0000
PIE	Pluviothermic index of Emberger	100*P/(tMc2-tmf2)	-0.0023***	0.0642	-0.0009*	0.0313	-0.0152	0.0027
Qe	Drought index of Baudiere	100*Pe/(tMc2-tmf2)	-0.0115	0.0238	-0.0043	0.0109	0.0568	0.0006
S1	Summer humidity index of Lara	(PVIII+PVIII)/(TVII-VIII)	-0.0004	0.0054	0.0000	0.0001	0.0169	0.0084
HCH	Henze-Dieckmann hydric continentality index	(PV+PVI+PVII)- (PVIII+PIX+PX)	-0.0006	0.000*	-0.0061**	0.0353	-0.6738***	0.1247
A	Angot hydric continentality index	(PIII+PIV+PV+PVI+PVII+PVIII +PIX)/(PX+PXI+PXII+PI+PII)	2.7188	0.0241	1.2388	0.0161	-32.4426	0.0033
DR	Humidity index of Dantín-Ravenga	100*T/P	0.7617***	0.0717	0.2426	0.0235	12.0286	0.0170
Altitude			-0.0005***	0.0707	-0.004***	0.1176	-0.0189	0.0839

Table A2: Correlation matrix of the climatic variables. Variables noted in bold are the ones selected in the regression models

	R	WR	**SR**	SMR	AR	**WT**	ST	SMT	**AT**	tmf	tMc	at	Atabs	**PCRA**	CPRE	G	Imae	IO	PH	**PIE**	Qe	S1	**HCH**	A
R	1.00																							
WR	0.92	1.00																						
SR	0.99	0.90	1.00																					
SMR	0.55	0.28	0.57	1.00																				
AR	0.98	0.86	0.99	0.63	1.00																			
WT	-0.61	-0.39	**−0.69**	-0.62	-0.66	1.00																		
ST	-0.64	-0.39	-0.70	-0.80	-0.70	0.92	1.00																	
SMT	-0.66	-0.44	-0.67	-0.84	-0.70	0.67	0.89	1.00																
AT	-0.59	-0.36	**−0.67**	-0.70	-0.66	0.97	**0.97**	0.78	1.00															
tmf	-0.52	-0.27	-0.60	-0.60	-0.59	0.98	0.87	0.59	0.93	1.00														
tMc	-0.60	-0.39	-0.61	-0.86	-0.64	0.59	0.82	0.96	0.70	0.51	1.00													
at	0.46	0.32	0.54	0.32	0.49	-0.86	-0.65	-0.30	-0.74	-0.89	-0.20	1.00												
Atabs	-0.12	-0.18	-0.04	-0.15	-0.09	-0.39	-0.13	0.22	-0.26	-0.49	0.35	0.71	1.00											
PCRA	-0.34	-0.56	**−0.34**	0.50	-0.24	**0.13**	-0.08	-0.20	**0.02**	0.05	-0.30	-0.33	-0.26	1.00										
CPRE	-0.25	-0.51	-0.22	0.61	-0.16	-0.15	-0.31	-0.35	-0.23	-0.22	-0.45	-0.04	-0.09	0.92	1.00									
G	0.57	0.32	0.59	0.98	0.63	-0.61	-0.82	-0.89	-0.72	-0.56	-0.93	0.26	-0.24	0.45	0.57	1.00								
Imae	0.62	0.37	0.64	0.97	0.68	-0.65	-0.86	-0.93	-0.75	-0.60	-0.93	0.30	-0.20	0.39	0.52	0.99	1.00							
IO	0.13	-0.09	0.15	0.79	0.23	-0.24	-0.49	-0.61	-0.36	-0.24	-0.70	-0.09	-0.33	0.78	0.79	0.78	0.75	1.00						
PH	0.57	0.31	0.60	0.98	0.64	-0.67	-0.85	-0.89	-0.76	-0.62	-0.92	0.33	-0.16	0.43	0.57	0.99	0.99	0.76	1.00					
PIE	0.85	0.69	**0.85**	0.80	0.87	**−0.63**	-0.81	-0.92	**−0.72**	-0.53	-0.90	0.30	-0.29	**0.02**	0.13	0.86	0.88	0.48	0.85	1.00				
Qe	0.59	0.35	0.60	0.96	0.65	-0.61	-0.83	-0.93	-0.72	-0.55	-0.96	0.24	-0.28	0.41	0.54	0.99	0.99	0.76	0.98	0.89	1.00			
S1	0.42	0.15	0.44	0.97	0.50	-0.53	-0.75	-0.83	-0.64	-0.51	-0.87	0.19	-0.23	0.62	0.70	0.97	0.95	0.87	0.96	0.74	0.95	1.00		
HCH	-0.11	-0.11	**−0.06**	-0.04	-0.15	**−0.38**	-0.24	0.00	**−0.31**	-0.38	0.01	0.56	0.46	**−0.24**	0.06	-0.04	-0.05	-0.21	0.00	**−0.10**	-0.04	-0.08	1.00	
A	-0.25	-0.54	-0.20	0.56	-0.15	-0.32	-0.41	-0.36	-0.38	-0.42	-0.41	0.18	0.15	0.78	0.94	0.51	0.48	0.64	0.54	0.10	0.48	0.64	0.24	1.00
DR	-0.86	-0.68	-0.91	-0.74	-0.90	0.87	0.90	0.81	0.88	0.80	0.75	-0.66	-0.08	0.13	-0.04	-0.75	-0.79	-0.35	-0.77	-0.87	-0.76	-0.63	-0.09	-0.11

Table A3: Principal components analysis of the climatic variables included in the regression model

	Axis 1	**Axis 2**
Standard deviation	2.084	1.369
Proportion of Variance	0.434	0.188
Cumulative Proportion	0.434	0.622
Variable scores		
SR	0.434	0.074
PCRA	−0.047	−0.040
PIE	0.425	−0.100
HCH	0.116	−0.162
WT	−0.419	−0.142
AT	−0.411	−0.162
SR*WT	−0.360	0.180
SR*PCRA	−0.030	−0.625
PCRA*WT	0.052	0.655
PIE*WT	0.369	0.237

Figure A1: Species richness at the forest scale. Background color represents altitude

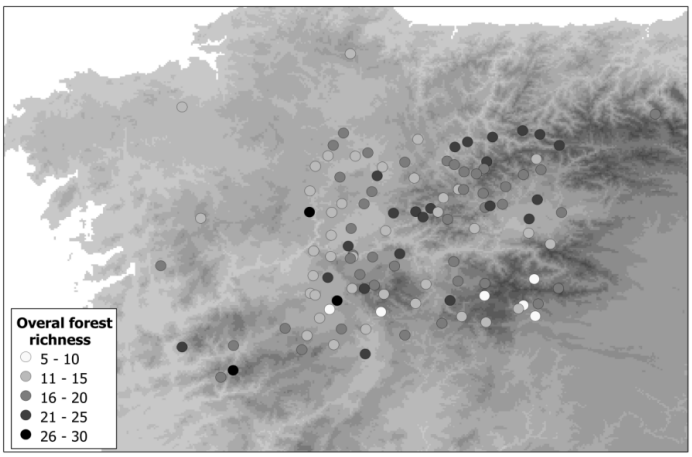


Figure A2: Relative weights of the models (y axis) over the position of the models ranked by their AIC value. Weights are computed as $\exp(-\Delta IC/2)$, where ΔIC is the difference in IC between a model and the best model, and they normalized so that they sum up to one

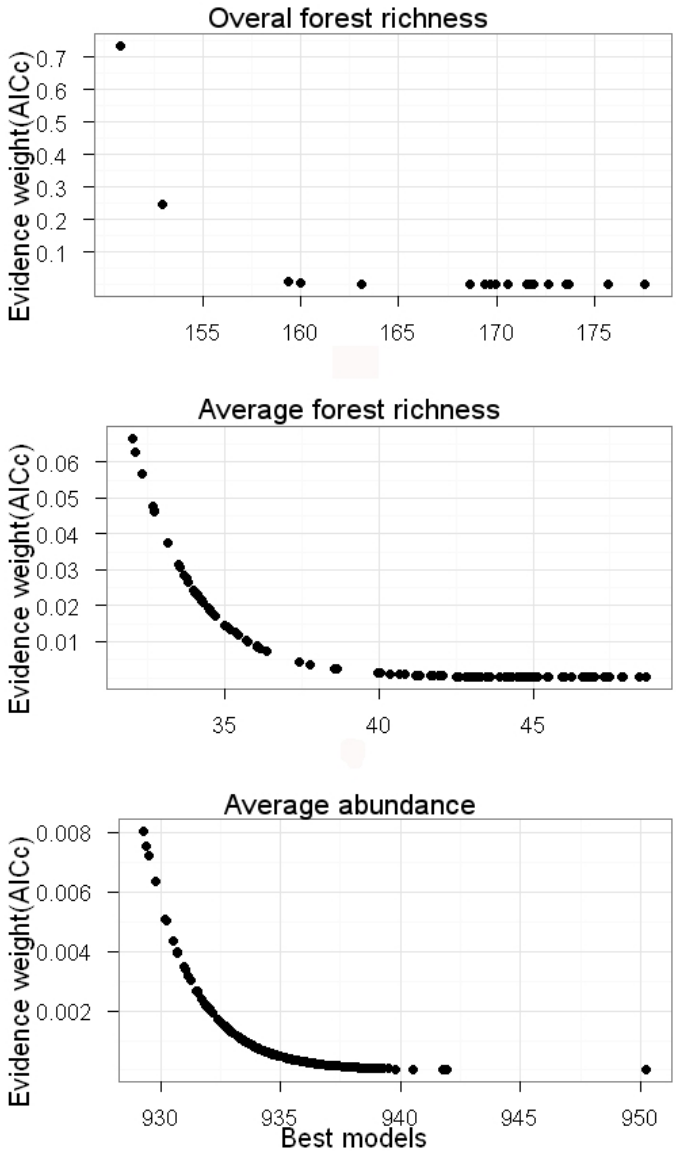


Figure A3: Relative weights (importance) of model terms. The weights are calculated using the whole set of possible models (18 for overall forest richness, 113 for average forest richness and 1421 for average abundance). Dark grey bars indicate the variables that were selected in the best model

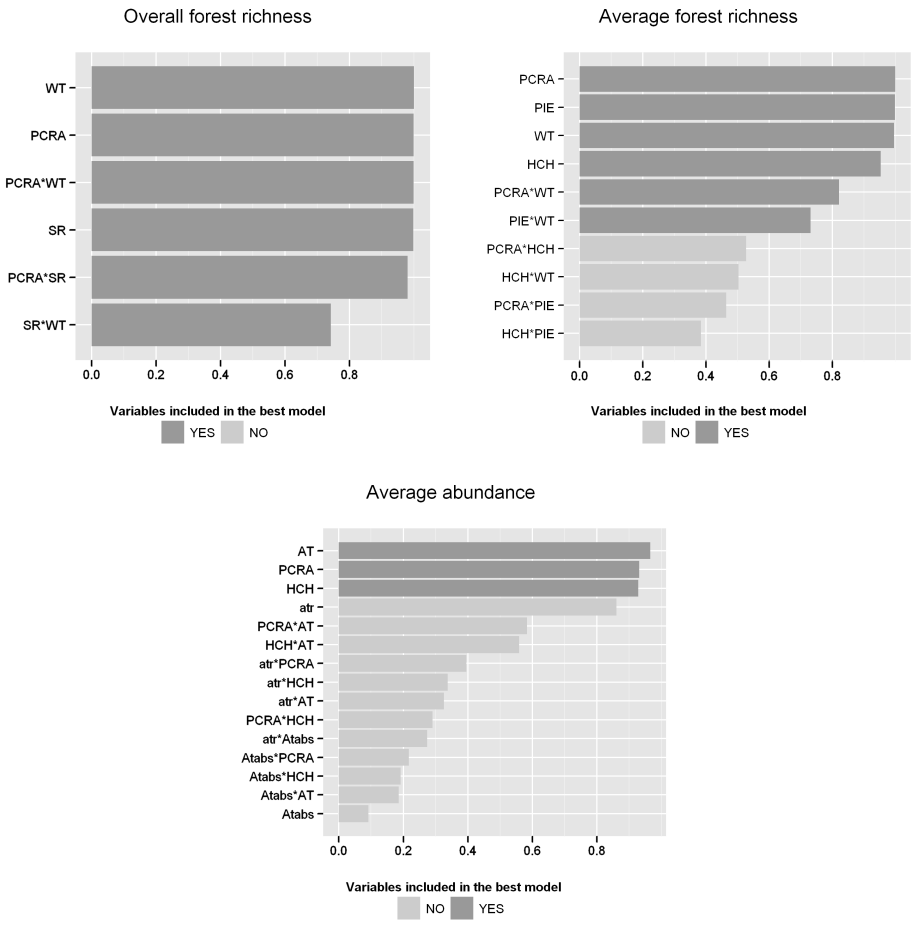


Figure A4: Venn diagrams depicting the results of the variation partitioning of richness into the independent effects of climate, topography, forest structure and region, as well as their overlap. U refers to the unexplained variation. Values <0.01 have been depicted in grey in order to make the figure easy to read

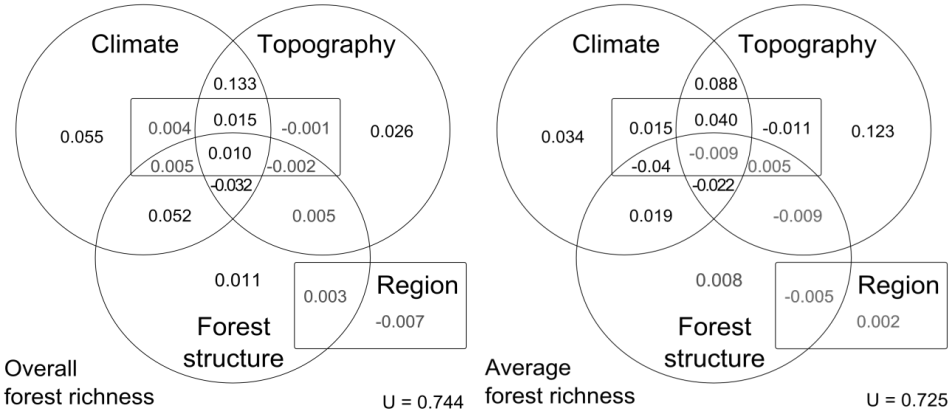


Figure A5: Histogram of the standard deviation of dbh per forest

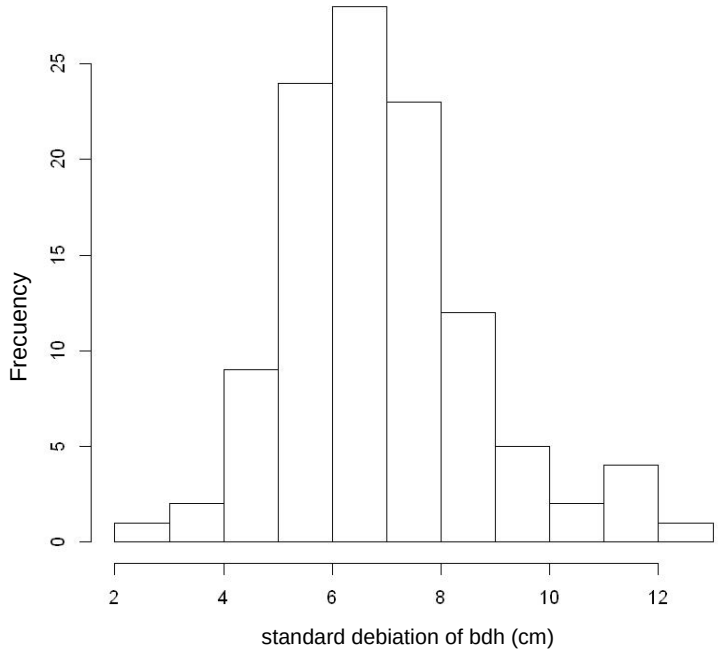
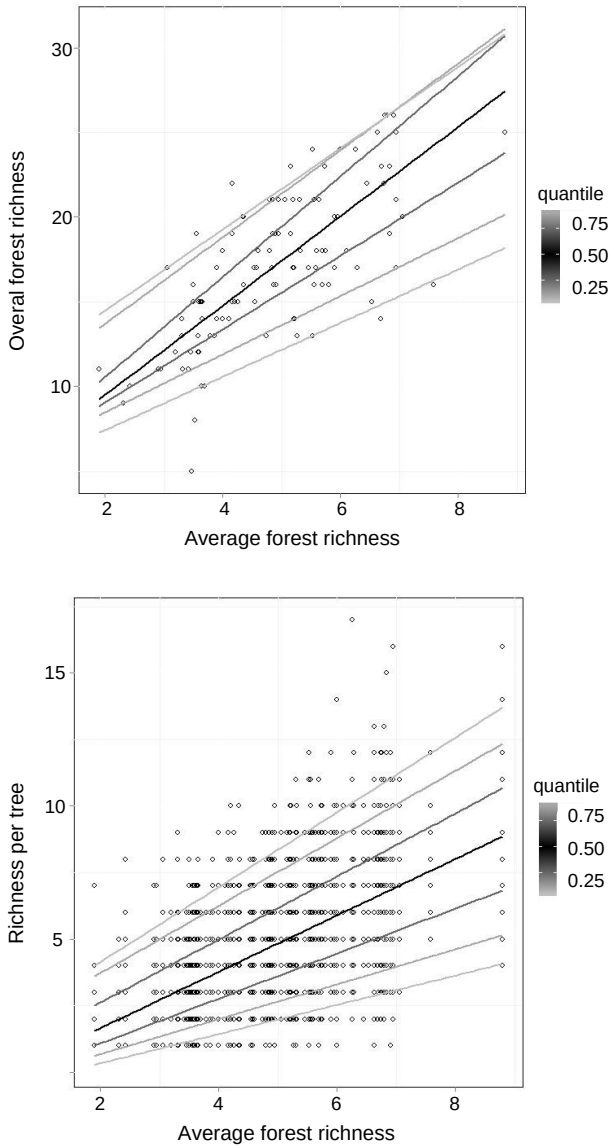


Figure A6: Quantile regression of the richness of epiphytic bryophytes at the forest and tree scales



Anexo B Material complementario al Capítulo 4

Supplementary material for Chapter 4

This supplementary material is primarily digital. The corresponding files can be found in the anexoB. The folder contains four files. On the one hand a compressed RAR file containing the original files of the distributions of species can be accessed clicking HERE. While the accompanying low resolution figures are recorded in this appendix (Figs B1 to B4). In addition, the file containing species presence absence data can be accessed (HERE) and environmental data can be found (pinchar AQUÍ). Finally, a word document (DOCX) including a detailed data dictionary for environmental database (click HERE). Additionally, the article associated to this chapter has been accepted for publication in Frontiers of Biogeography so the databases and related files can be downloaded from the repository of the journal.

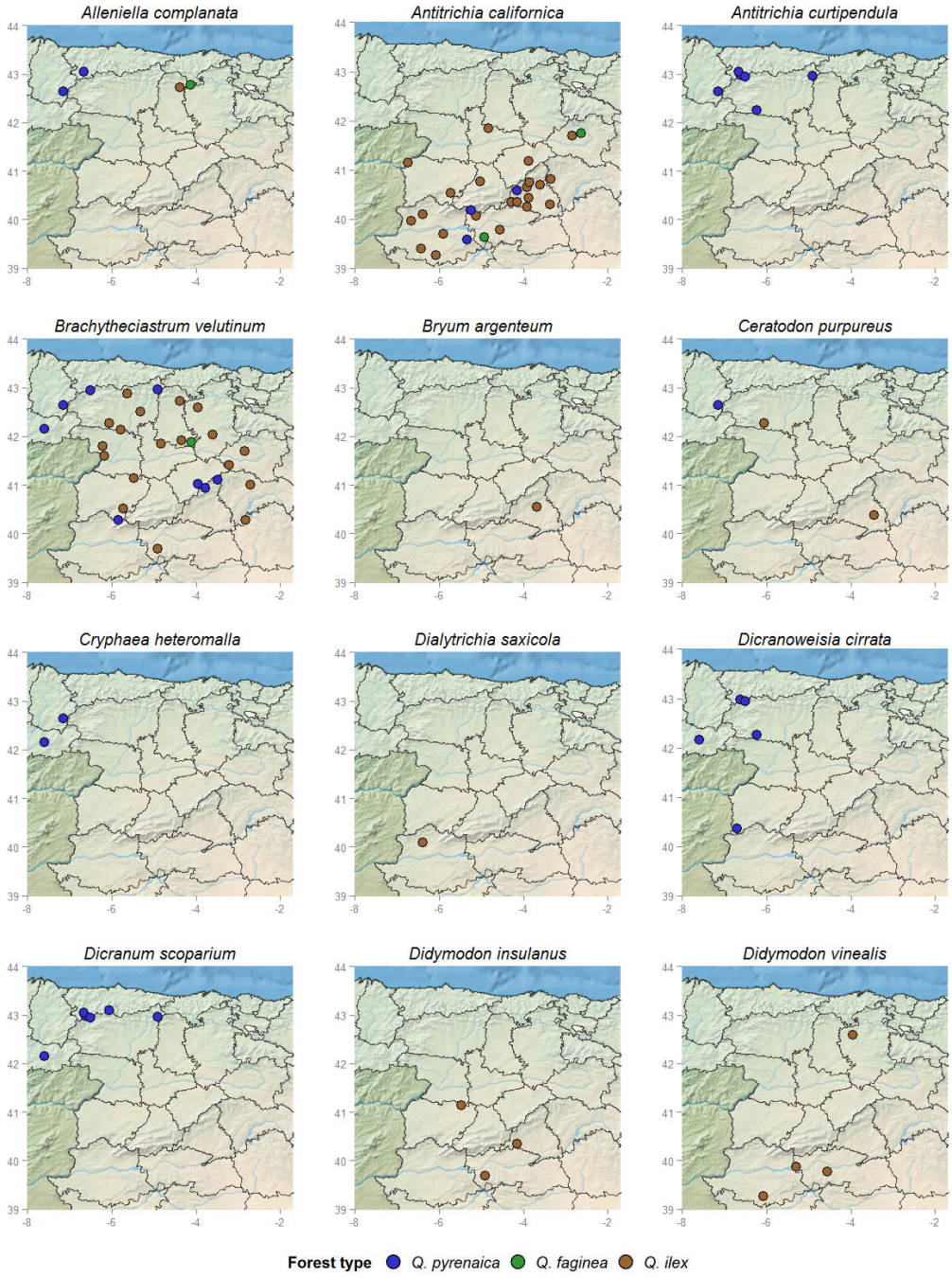


Figure B1: Distribution maps of some of the species

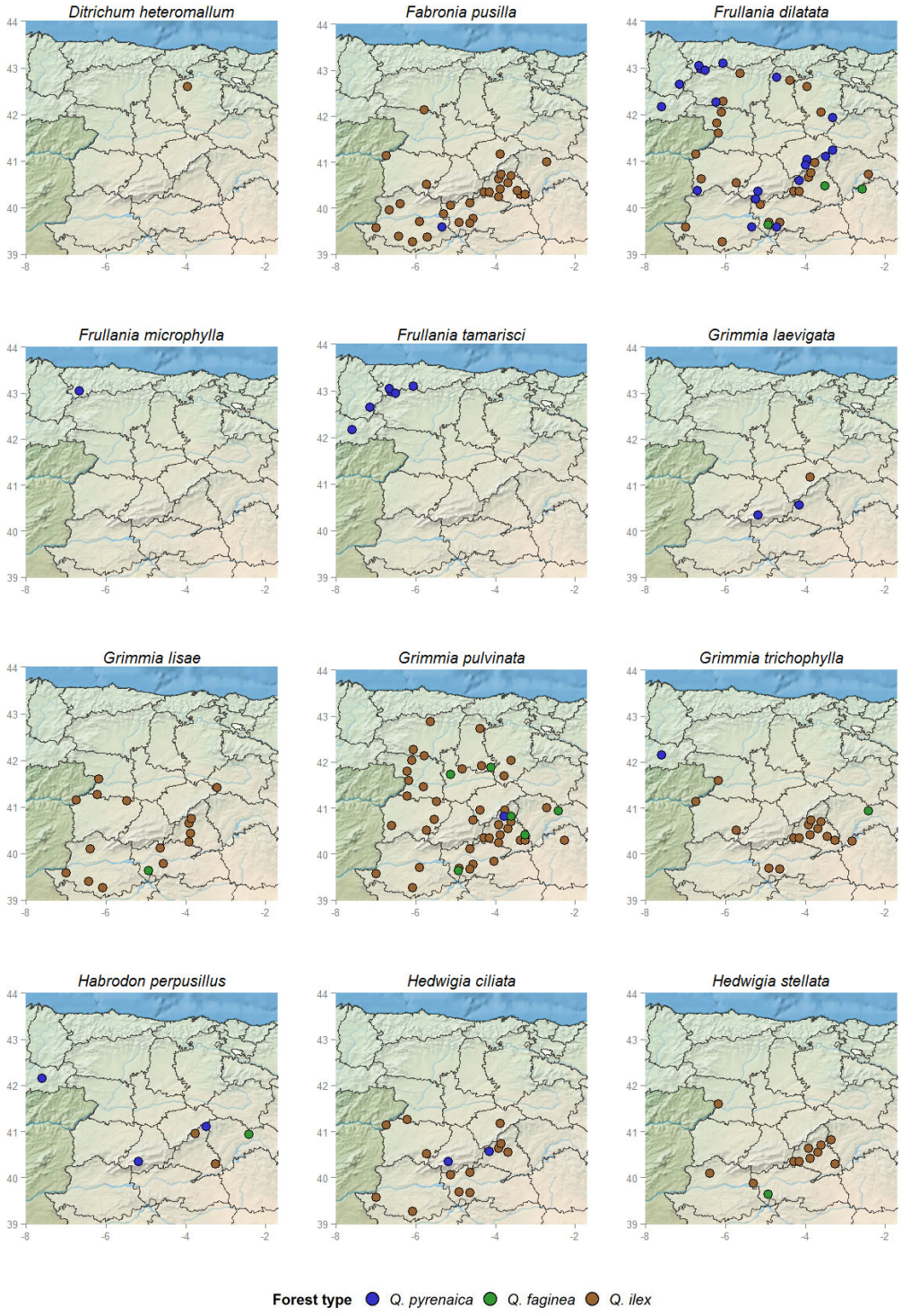


Figure B2: Distribution maps of some of the species

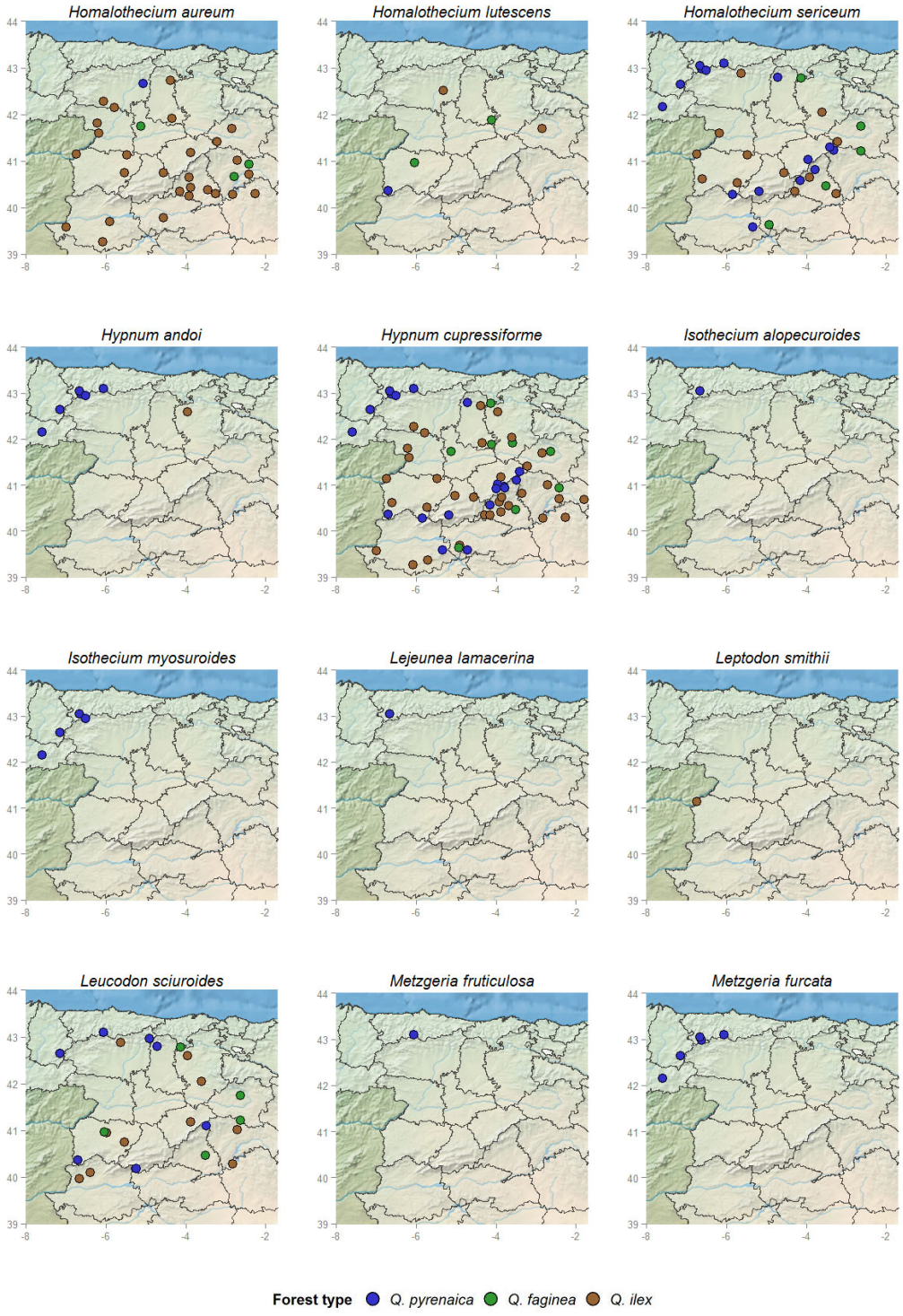


Figure B3: Distribution maps of some of the species

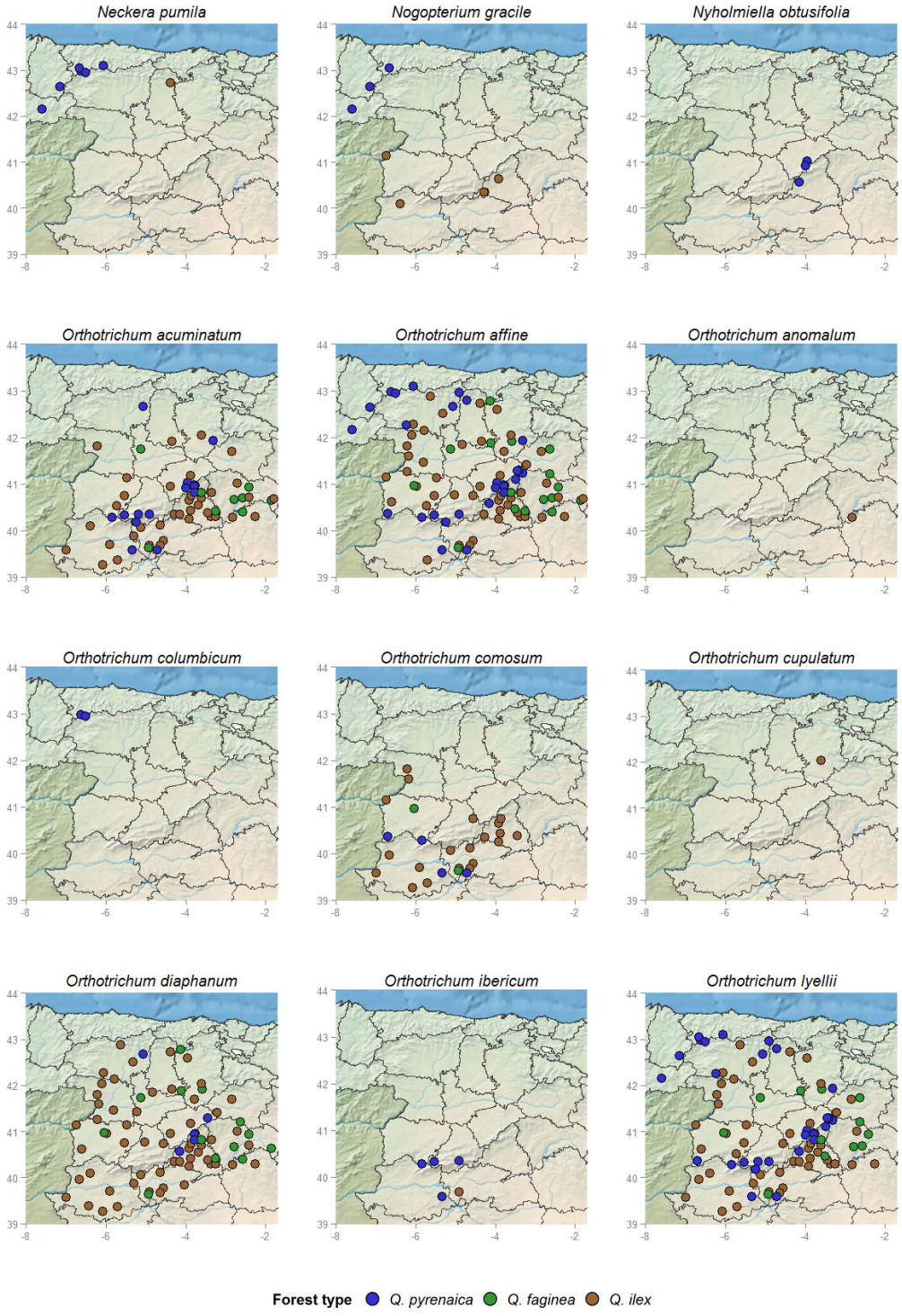


Figure B4: Distribution maps of some of the species

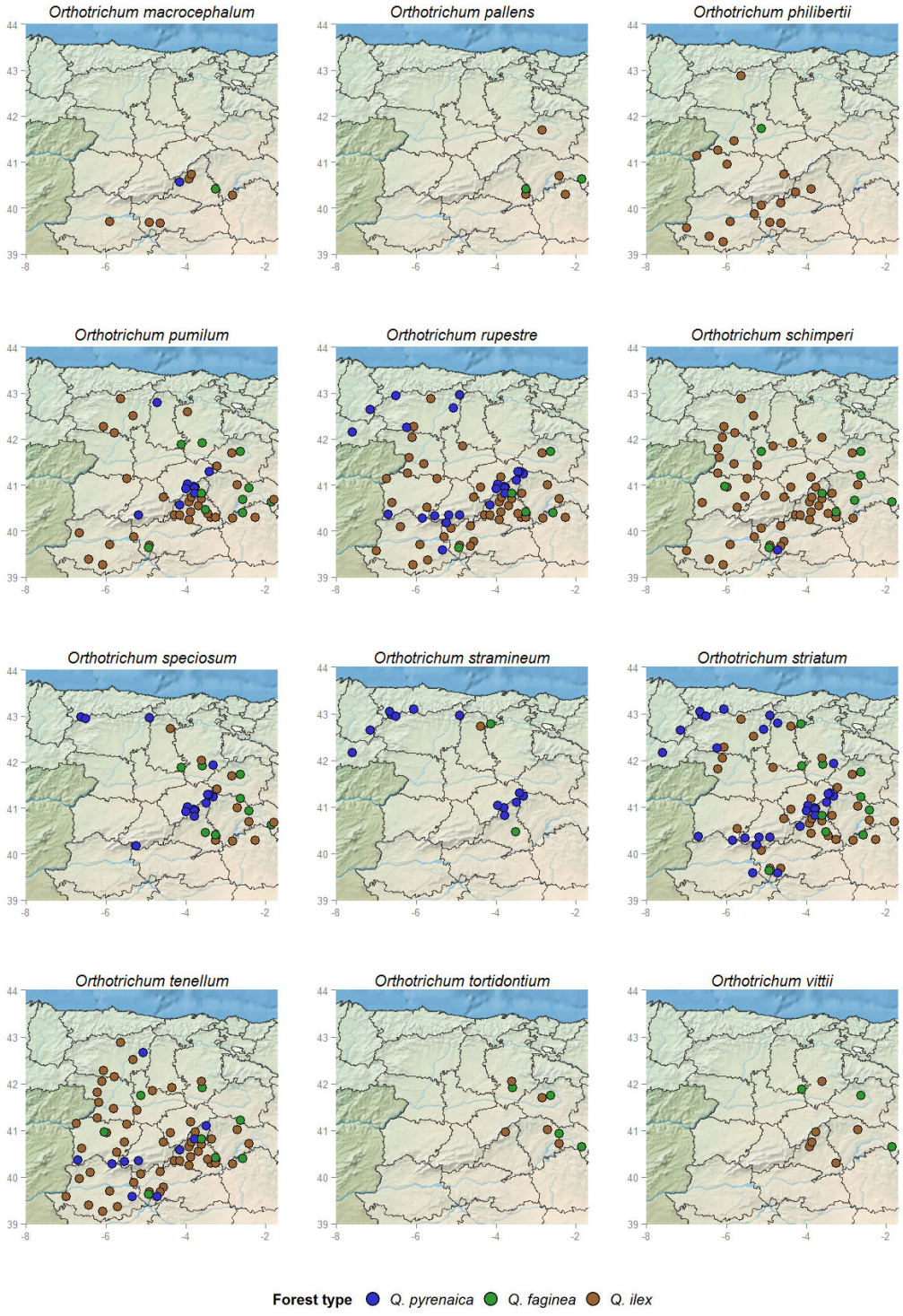


Figure B5: Distribution maps of some of the species

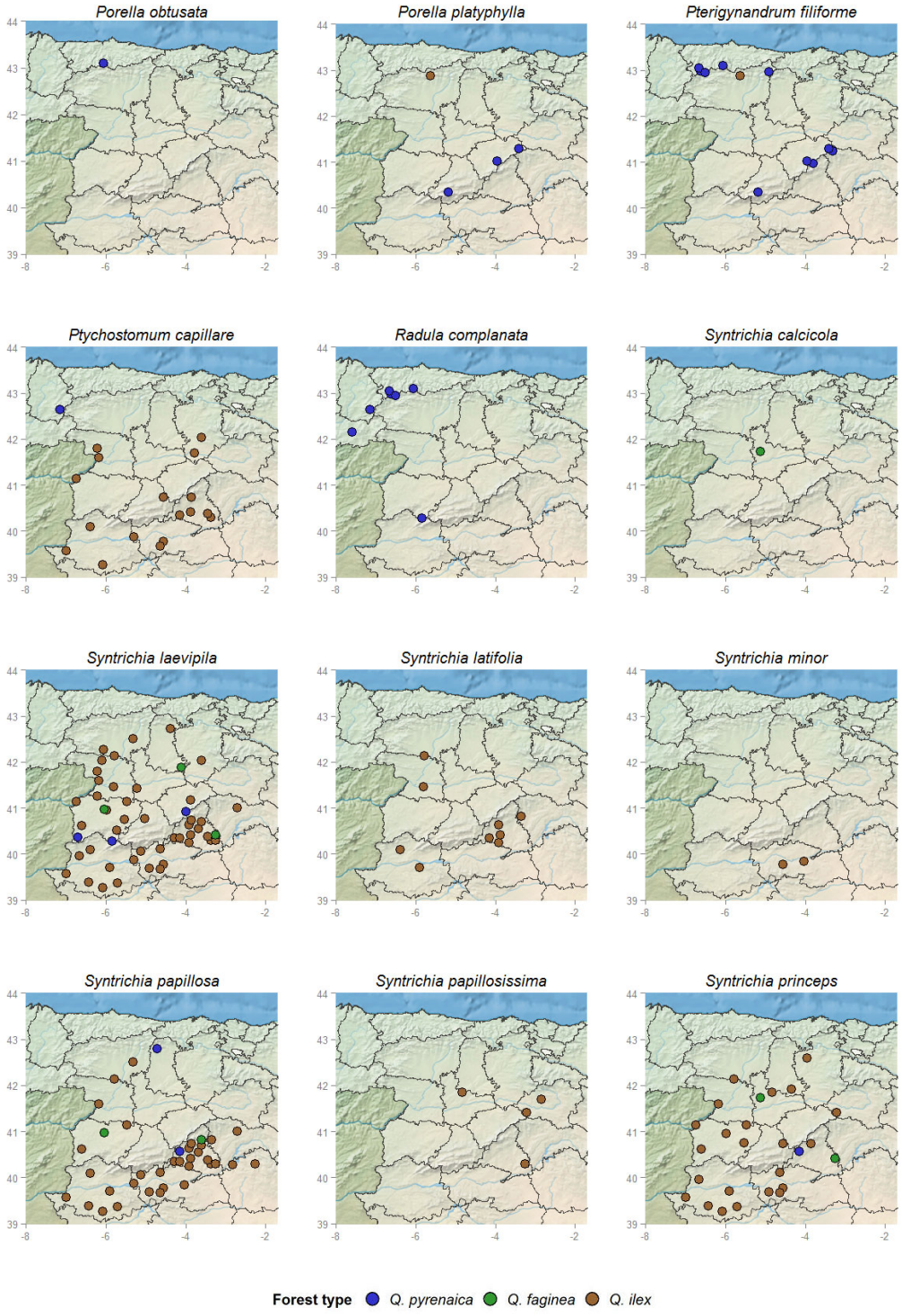


Figure B6: Distribution maps of some of the species

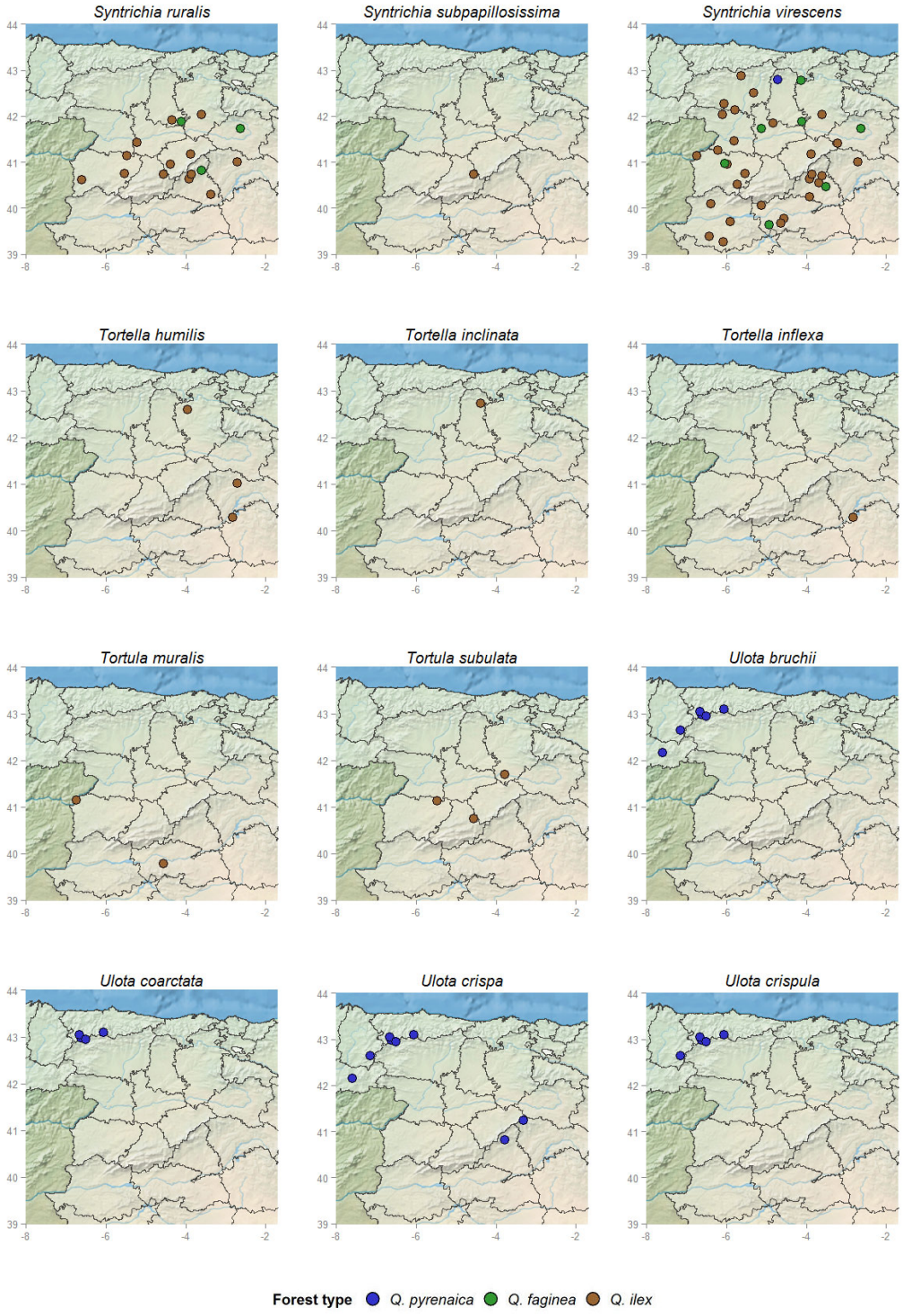


Figure B7: Distribution maps of some of the species

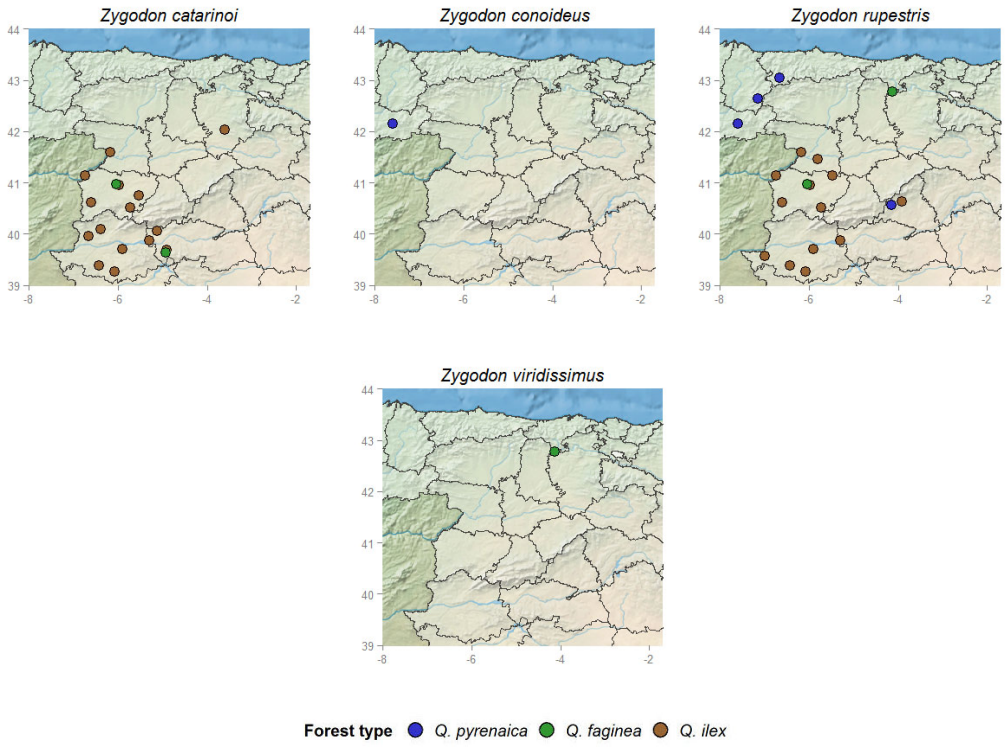


Figure B8: Distribution maps of some of the species

Anexo B.1 **Distribution groups of species**

The bryophyte data recorded allows mapping the distributions of all species in the study area. The visual analysis of these distributions reveals some common patterns, which seem to follow the main climatic and topographic gradients of the study area. Based on expert knowledge we have classified the species of the database according to their distributional patterns or chorologic tendencies. These groups are not intended to be closed units but rather loose groups that are representative of the most common patterns of distributions in the study area. Note that the patterns described below are based just on the distribution of the species as epiphytes; some of the species also colonize a diverse set of micro-environments including soils and rock outcrops and so their general distribution including all the micro-environments they colonize might be more extensive and show a different pattern.

Group I) Species that occur almost exclusively in the NW of the study area under a climate with humid or very humid summers. Apart from the selected examples *Dicranum scoparium* and *Frullania tamarisci*, other 15 species would pertain to this group (see distribution maps): *Alleniella complanata, Cryphaea heteromalla, Dicranum scoparium, Frullania microphylla, F. tamarisci, Isothecium alopecuroides, I. myosuroides, Lejeunea lamacerina, Metzgeria fruticulosa, Orthotrichum columbicum, Ulota bruchii, U. coarctata, U. crispula, Zygodon conoideus*, and *Z. viridissimus*. At least other six species (*Antitrichia curtipendula, Dicranoweisia cirrata, Hypnum andoi, Metzgeriafurcata, Neckera pumila,* and*Ulota crispa)* of this group extend their distribution towards the south taking advantage of the relatively wet conditions of the mountainous areas under Mediterranean climate.

Group II) Species whose distribution is mostly restricted to areas with a marked drought period in summer. These species form a diverse group that include several distinctive trends:

Group IIa) Species that prefer milder conditions within the Mediterranean region, usually taking advantage of higher elevations and mesic conditions such as favourable slopes, or river vicinity. These species can be exemplified by (see distribution maps) *Orthotrichum acuminatum* and *O. ibericum*, and also include *Homalothecium lutescens, Orthotrichum tortidontium, O. vittii, S. papillosissima*, and*S. ruralis.*

Species distributed mainly in the mild continental zone, that become less frequent in inner continental areas where they appear mostly in localities where the continentality is moderated by some atlantic influence. *Orthotrichum philibertii* and *Zygodon catarinoi* are good examples from this group that also includes Antitrichia californica, Dialytrichia saxicola, Fabronia pusilla, Grimmia lisae, G. trichophylla, Hedwigia ciliata, H. stellata, Leptodon smithii, Orthotrichum comosum, O. macrocephalum, Syntrichia minor, and black *S. papillosa*.

Group IIb) Species that are widely distributed across both nothern and southern Iberian plateaus, and are present even in the most xeric and continental locations of the study area, being frequent in most forests of the northern plateau. Apart from *O. schimperi* and *O. tenellum*, at least six other species pertain to this group: *Grimmia pulvinata, Homalothecium aureum, Syntrichia laevipila, S. latifolia, S. princeps,* and *S. virescens.*

Group IIc) Species that are widely distributed across both northern and southern

Iberian plateaus, and are present even in the most xeric and continental locations of the study area. Apart from *O. schimperi* and *O. tenellum*, at least six other species pertain to this: *Grimmia pulvinata, Homalothecium aureum, Syntrichia laevipila, S. latifolia, S. princeps,* and *S. virescens.*

Group III) Species that are distributed in areas under both Atlantic and Mediterranean climates, and are therefore indifferent to summer drought. This is a diverse group that can be subdivided into three subgroups according to their distribution patterns:

Group IIIa) The species included in this subgroup occupy localities that harbor mesic conditions and thus are present in the northwest of the study area under Atlantic climate and in areas with relatively high precipitations under Mediterranean climate. Most of the species are common in mountainous areas but also colonize forests at lower heights as long as they have enough precipitations. By contrast, they are absent from the most xeric locations of the Iberian plateaus. *Frullania dilatata* and *O. rupestre.* The group also includes: *Brachytheciastrum velutinum, Habrodon perpusillus, Homalothecium sericeum, Hypnum cupressiforme, Leucodon sciuroides, Nogopterium gracile, Nyholmiella obtusifolia, Orthotrichum affine, O. lyellii, O. pallens, O. pumilum, O. striatum, Porella obtusata, P. platyphylla, Radula complanata,* and *Zygodon rupestris.*

Group IIIb) This is a small subgroup formed by montane species that are found in relatively high altitudes. Even if the distribution in the study area of some of these species may look similar to the Group Ib, the species here concerned are not Atlantic bryophytes that take refuge in particular ecological situations occasionally found in Mediterranean mountains; they are orophylous species, more or less equally spread in both Atlantic and Mediterranean mountains. This pattern is much clearer taking into account the whole distribution of these species as epiphytes in the Iberian Peninsula. Representative examples of the group are *Orthotrichum speciosum* and*O. stramineum,* but also *Pterigynandrum filiforme* is included here.

Group IIIc) This subgroup includes species that grow mostly in xeric conditions. Therefore, in the wettest locations of the study area they tend to occupy exposed trees or open forests while they are common in the localities under the Mediterranean climate that harbour predominantly dry conditions. The distribution of these species may look similar to the ones in group IIc, however the species included in this group have a considerable number of presences in the Cantabrian range while the species in group IIc are mostly absent from that area. Only two species pertain to this group: *O. diaphanum* and *Ptychostomum capillare.*

Group IV) This group includes the species that are occasional as epiphytes and since they have been rarely recorded they cannot be ascribed to any specific pattern (distribution maps in Appendix 1): *Bryum argenteum, Ceratodon purpureus, Didymodon insulanus, Didymodon vinealis, Ditrichum heteromallum, Grimmia laevigata, Orthotrichum anomalum, O. cupulatum, Syntrichia calcicola, S. subpapillosissima, Tortella humilis, T. inclinata, T. inflexa, Tortula muralis,* and *T. subulata.*

Anexo C **Material complementario al Capítulo 5**

Supplementary material for Chapter 5

Localidades de muestreo en las que se detalla, número de localidad, provincia, término municipal, coordenadas geográficas y altitud.

1 Asturias: Teverga; Melojar; 43º 05' 56" N 6º 03' 06" W, 831 m
2 Asturias: Cangas de Narcea; Melojar; 42º 58' 57" N 6 º 37' 37" W, 762 m
3 Asturias: Cangas de Narcea; Melojar; 43º 02' 39" N 6º 39' 08" W, 685 m
4 Asturias: Degaña; Melojar; 42º 56' 39" N 6º 30' 46" W, 1027 m
5 Ávila: Solana de Rioalmar; Encinar; 40º 45' 50" N 5º 01' 10" W, 1036 m
6 Ávila: Tolbaños; Encinar; 40º 44' 21" N 4º 33' 12" W, 938 m
7 Ávila: Serranillos; Melojar; 40 º 20' 15" N 4º 54' 18" W, 1276 m
8 Ávila: Candeleda; Melojar; 40º 10' 37" N 5º 14' 08" W, 763 m
9 Ávila: Poyales del Hoyo; Melojar; 40º 20' 21" N 5º 10' 37" W, 633 m
10 Ávila: Navalonguilla; Melojar; 40º 19' 29" N 5º 31' 19" W, 1130 m
11 Burgos: Castrillo de la Vega; Encinar; 41º 41' 55" N 3º 47' 09" W, 812 m
12 Burgos: Pinilla Trasmonte; Quejigar; 41º 54' 53" N 3º 35' 00" W, 988 m
13 Burgos: Pinilla de los Barruecos; Melojar; 41º 55' 44" N 3º 18' 35" W, 1032 m
14 Burgos: Quintanilla del Agua; Encinar; 42º 02' 29" N 3º 36' 20" W, 893 m
15 Burgos: Boa de Villadiego; Encinar; 42º 35' 05" N 3º 56' 47" W, 995 m
16 Burgos: Monasterio de Rodilla; Quejigar; 40º 27' 47" N 3º 30' 39" W, 950 m
17 Cáceres: El Gordo; Encinar; 39º 52' 19" N 5º 18' 20" W, 364 m
18 Cáceres: Jaraicejo; Encinar; 39º 42' 04" N 5º 54' 30" W, 428 m
19 Cáceres: Conquista de la Sierra; Encinar; 39º 21' 35" N 5º 42' 50" W, 634 m
20 Cáceres: Salvatierra de Santiago; Encinar; 39º 15' 31" N 6º 04' 49" W, 469 m
21 Cáceres: Cáceres; Encinar; 39º 23' 22" N 6º 25' 30" W, 363 m
22 Cáceres: Membrío; Encinar; 39º 34' 26" N 6º 59' 58" W, 213 m
23 Cáceres: Guijo de Galisteo; Encinar; 40º 05' 53" N 6º 23' 51" W, 419 m
24 Cáceres: Navatrasierra; Melojar; 39º 34' 54" N 5º 20' 38" W, 1018 m
25 Cáceres: Hervás; Melojar; 40º 16' 47" N 5º 50' 17" W, 940 m
26 Cáceres: Casillas de Coria; Encinar; 39º 57' 23" N 6º 39' 29" W, 336 m
27 Cuenca: Torralba; Encinar; 40º 17' 44" N 2º 14' 51' W, 1212 m
28 Guadalajara: Trillo; Quejigar; 40º 41' 18" N 2º 34' 34" W, 804 m
29 Guadalajara: Valtablado del Río; Encinar; 40º 42' 16" N 2º 24' 38" W, 992 m
30 Guadalajara: Megina; Quejigar; 40º 38' 20" N 1º 50' 55" W, 1221 m
31 Guadalajara: Traíd; Encinar; 40º 40' 42" N 1º 47' 24" W, 1361 m
32 Guadalajara: Alcohujate; Quejigar; 40º 23' 27" N 2º 34' 7" W, 926 m
33 Guadalajara: El Cardoso; Melojar; 41º 05' 51" N 3º 28' 46" W, 1319 m
34 Guadalajara: Cantalojas; Melojar; 41º 13' 55" N 3º 18' 52" W, 1458 m
35 Guadalajara: Almonacid de Zorita; Encinar; 40º 16' 26" N 2º 49' 45" W, 808 m
36 Guadalajara: Budia; Quejigar; 40º 39' 32" N 2º 46' 54" W, 1049 m
37 Guadalajara: Sotodosos; Quejigar; 40 º 55' 56" N 2º 24' 53" W, 1137 m
38 Guadalajara: Sigüenza; Encinar; 41º 00' 16" N 2º 42' 19" W, 1032 m
39 Guadalajara: Sienes; Quejigar; 41º 12' 32" N 2º 37' 14" W, 1212 m
40 Guadalajara: Villaseca de Uceda; Encinar; 40º 49' 05" N 3º 20' 48" W, 905 m
41 León: Villomar; Encinar; 42º 30' 40" N 5º 19' 25" W, 830 m
42 León: Valderey; Encinar; 42º 16' 25" N 6º 03' 57" W, 849 m
43 León: Santa Lucía; Encinar; 42º 52' 17" N 5º 37' 42" W, 1186 m
44 León: Alija del Infantado; Encinar; 42º 08' 04" N 5º 47' 26" W, 757 m
45 León: Almanza; Melojar; 42º 40' 02" N 5º 04' 11" W, 974 m
46 León: Boca de Huergano; Melojar; 42º 57' 56" N 4º 54' 17" W, 1247 m
47 León: Castrocontrigo; Melojar; 42º 15'

26” N 6º 13’ 30” W, 1145 m
48 Lugo: Seoane do Caurel; Melojar; 42º 38’ 19” N 7 º 08’ 25” W, 600 m
49 Madrid: Arganda; Encinar; 40º 17’ 45” N 3º 22’ 26” W, 732 m
50 Madrid: Madrid; Encinar; 40º 32’ 26” N 3º 41’ 03” W, 709 m
51 Madrid: Loeches; Encinar; 40º 22’ 50” N 3º 26’ 13” W, 639 m
52 Madrid: Hoyo de Manzanares; Encinar; 40º 38’ 12” N 3º 54’ 17” W, 1046 m
53 Madrid: Boadilla del Monte; Encinar; 40º 25’ 11” N 3º 52’ 22” W, 703 m
54 Madrid: Batres; Encinar; 40º 14’ 22” N 3º 55’ 11” W, 625 m
55 Madrid: Carabaña; Encinar; 40º 17’ 18” N 3º 14’ 44” W, 799 m
56 Madrid: Navas del Rey; Encinar; 40º 20’ 27” N 4º 15’ 39” W, 568 m
57 Madrid: San Agustión de Guadalix; Encinar; 40º 41’ 59” N 3º 35’ 41” W, 792 m
58 Madrid: Manzanares el Real; Encinar; 40º 44’ 17” N 3º 50’ 46” W, 915 m
59 Madrid: San Martín de Valdeiglesias; Encinar; 40º 20’ 45” N 4º 17’ 31” W, 700 m
60 Madrid: El Escorial; Melojar; 40º 34’ 07” N 4º 09’ 05” W, 1038 m
61 Madrid: Lozoya; Encinar; 40º 57’ 13” N 3º 45’ 30” W, 1206 m
62 Madrid: Lozoya; Melojar; 40º 58’ 11” N 3º 47’ 58” W, 1281 m
63 Madrid: Lozoya; Melojar; 40º 56’ 33” N 3º 46’ 03” W, 1086 m
64 Madrid: Miraflores; Melojar; 40º 48’ 39” N 3º 46’ 58” W, 1220 m
65 Madrid: Redueña; Quejigar; 40º 48’ 38” N 3º 36’ 23” W, 814 m
66 Madrid: Corpa; Quejigar; 40º 24’ 54” N 3º 14’ 49” W, 844 m
67 Madrid: Villamantilla; Encinar; 40º 20’ 22” N 4º 09’ 04” W, 550 m
68 Orense: Vilar de Barrio; Melojar; 42º 9’ 33” N 7º 35’ 54” W, 827 m
69 Palencia: Santibañez de Ecla; Encinar; 42º 43’ 35” N 4º 22’ 16” W, 1070 m
70 Palencia: Pomar de Valdivia; Quejigar; 42º 46’ 08” N 4º 08’ 04” W, 1070 m
71 Palencia: Valle del Cerrato; Encinar; 41º 54’ 41” N 4º 20’ 24” W, 885 m
72 Palencia: Santibañez de la Peña; Melojar; 42º 47’ 30” N 4º 42’ 31” W, 1135 m
73 Palencia: Montemayor; Quejigar; 41º 52’ 37” N 4º 06’ 16” W, 892 m
74 Salamanca: Mieza; Encinar; 41º 08’ 17” N 6º 43’ 52” W, 572 m
75 Salamanca: Tardáguila; Encinar; 41º 07’ 54” N 5º 27’ 58” W, 886 m
76 Salamanca: La Orbada; Encinar; 41º 07’ 54” N 5º 27’ 58” W, 852 m
77 Salamanca: Puebla; Encinar; 40º 31’ 16” N 5º 43’ 08” W, 1036 m
78 Salamanca: Ejeme; Encinar; 40º 44’ 44” N 5º 31’ 35” W, 759 m
79 Salamanca: Saelices chico; Encinar; 40º 36’ 56” N 6º 36’ 04” W, 642 m
80 Salamanca: Canillas de Abajo; Encinar; 40º 56’ 42” N 5º 58’ 36” W, 739 m
81 Salamanca: Fuenteguinaldo; Melojar; 40º 21’ 38” N 6º 42’ 18” W, 875 m
82 Salamanca: Tabera de Abajo; Quejigar; 40º 57’ 56” N 6º 02’ 22” W, 823 m
83 Segovia: Collado Hermoso; Melojar; 41º 01’ 32” N 3º 56’ 40” W, 1172 m
84 Segovia: San Ildefonso; Melojar; 40º 54’ 53” N 3º 59’ 27” W, 1251 m
85 Segovia: Arevalillo de Cega; Encinar; 41º 10’ 24” N 3º 52’ 45” W, 972 m
86 Segovia: Riaza (La Quesera); Melojar; 41º 17’ 35” N 3º 24’ 44” W, 1562 m
87 Segovia: Riaza; Melojar; 41º 16’ 59” N 3º 26’ 35” W, 1420 m
88 Segovia: Marazoleja; Encinar; 40º 56’ 44” N 4º 22’ 47” W, 949 m
89 Soria: Tiermes; Encinar; 41º 24’ 19” N 3º 12’ 33” W, 1163 m
90 Soria: Blacos; Encinar; 41º 41’ 42’ N 2º 50’ 10” W, 763 m
91 Soria: Villaciervos; Quejigar; 41º 44’ 14” N 2º 37’ 42” W, 1146 m
92 Toledo: Toledo; Encinar; 39º 50’ 46” N 4º 01’ 16” W, 588 m
93 Toledo: El Carpio; Encinar; 39º 46’ 35” N 4º 33’ 15” W, 502 m
94 Toledo: Los Navalmorales; Encinar; 39º 40’ 35” N 4º 37’ 30” W, 907 m
95 Toledo: Belvís de la Jara; Encinar; 39º 40’ 54” N 4º 54’ 23” W, 746 m
96 Toledo: Navalcán; Encinar; 40º 03’ 16” N 5º 07’ 44” W, 401 m
97 Toledo: Garciotum; Encinar; 40º 06’ 55” N 4º 38’ 28” W, 586 m
98 Toledo: Navalucillos; Melojar; 39º 35’ 8” N 4º 42’ 29” W, 818 m
99 Toledo: Robledo del Mazo; Quejigar; 39º 38’ 02” N 4º 55’ 39” W, 907 m
100 Valladolid: Castronuño; Encinar; 41º 25’ 17” N 5º 12’ 47” W, 607 m
101 Valladolid: Villalba de los Alcores; Encinar; 41º 50’ 32” N 4º 49’ 29” W, 798 m
102 Valladolid: Castromonte; Quejigar; 41º 44’ 14” N 5º 07’ 28” W, 840 m
103 Zamora: El Perdigón; Encinar; 41º 27’ 11” N 5º 48’ 39” W, 723 m
104 Zamora: Salce; Encinar; 41º 15’ 32” N

6º 12’ 38” W, 751 m

105 Zamora: Fonfría; Encinar; 41º 35’ 21” N 6º 09’ 56” W, 714 m

106 Zamora: Riofrío de Aliste; Encinar; 41º 48’ 07” N 6º 12’ 38” W, 814 m

107 Zamora: San Pedro de Ceque; Encinar; 42º 02’ 19” N 6º 05’ 56” W, 791 m

Anexo D **Material complementario al Capítulo 6**

Supplementary material for Chapter 6

Table D1: Detailed description of the environmental variables used in this work

Category	Subcategory	Variable	Description	Scale	Unit	Range
Meso-environment	Climate	Annual Precipitation	Annual rainfall values extracted from Hijmans et al 2004	Forest	mm per year	363-776
Meso-environment	Climate	Annual Mean Temperature	Average temperature per year extracted from Hijmans et al 2004	Forest	^{o}C	8.7-16.9
Meso-environment	Climate	Temperature Seasonality	Standard variation of temperature * 100 extracted from Hijmans et al 2004	Forest	Unitless	-
Meso-environment	Topography	Slope	Visually estimated in the field	Forest	Degrees	0-40
Meso-environment	Forest management	Forest history	Forests were classified based on aerial photographs. Three categories: 1) forested if the forest had a similar structure in 1960 than nowadays, 2) degraded if the forest had a more opened or degraded structure and 3) strongly degraded if the forest had a very opened or shrub-like structure	Forest		Three categor-ies
Meso-environment	Forest management	Forest percentage	The percentage of a circle of 10km of diameter around the sampling point that is covered by forests according to the forestry map	Forest	%	20.7-94.9
Meso-environment	Forest structure	Canopy cover	Percentage of forest floor covered by the crowns of the trees. Estimated visually in the field	Stand	%	10-100
Meso-environment	Forest structure	Tree density	Estimated by applying the formula N (trees/ha)= (10.000*5,5) Where d is the distance to the sixth closest tree to the center of the stand (see figure in Appendix S2) /(π * d)	Stand	trees/ha	22.2-2402.6
Micro-environment	Tree charac-teristics	Bark roughness	Average of the two deepest furrows in the north and south sides of a tree. Measured at breast height	Tree	mm	3-67
Micro-environment	Tree charac-teristics	Diameter	Diameter at breast height (1.50m) measured with a DendroFlexómetro that uses a Biltmore scale	Tree	cm	10-50
Micro-environment	Tree charac-teristics	Canopy depth	Calculated by subtracting the total height of the tree to the height at which the canopy starts. Height was calculated using a DendroFlexómetro	Tree	m	0.6-11.3
Micro-environment	Tree charac-teristics	Transmitted light	The amount of light that passes through the canopy. To calculate it we took two hemispherical canopy photographs at 1 meter height and a distance of 50 cm from the trunk surface at the North and South faces of each tree with an Olympus SP590-UZ and a fisheye lens. Then we estimated the % of surface covered by the canopy and the transmitted light with GLA software taking into account the geographic position, cloudiness index (kt), spectral fraction (sf), beam fraction (bf) and topography of the site. Data on bf for each site was extracted from PGIVS maps Kt and sf were derived from bf using the formulae on GLA user manual	Tree	Mol/m2* day	2.7-22.6

Table D2: Species list

Species	Author
Alleniella complanata	(Hedw.) S.Olsson, Enroth & D.Quandt
Antitrichia californica	Sull.
Bartramia rosamrosiae	Damayanti, J. Muñoz, J.-P. Frahm & D. Quandt
Brachytheciastrum velutinum	Ignatov & Huttunen
Ceratodon purpureus	(Hedw.) Brid.
Dialytrichia saxicola	(Lamy) M.J.Cano
Didymodon insulanus	(De Not.) M.O.Hill
Didymodon vinealis	(Brid.) R.H.Zander
Fabronia pusilla	Raddi
Frullania dilatata	(L.) Dumort.
Grimmia lisae	De Not.
Grimmia pulvinata	(Hedw.) Sm.
Grimmia trichophylla	Grev.
Hedwigia ciliata	(Hedw.) P.Beauv.
Hedwigia stellata	Hedenäs
Homalothecium aureum	(Spruce) H.Rob.
Homalothecium lutescens	(Hedw.) H.Rob.
Homalothecium sericeum	(Hedw.) Schimp.
Hypnum cupressiforme	Hedw.
Leucodon sciuroides	(Hedw.) Schwägr.
Neckera pumila	Hedw.
Nogopterium gracile	(Hedw.) Crosby & W.R.Buck
Orthotrichum acuminatum	H.Philib.
Orthotrichum affine	Schrad. ex Brid.
Orthotrichum comosum	F. Lara, R. Medina & Garilleti
Orthotrichum cupulatum	Hoffm. ex Brid.
Orthotrichum diaphanum	Schrad. ex Brid.
Orthotrichum ibericum	F.Lara & Mazimpaka
Orthotrichum lyellii	Hook. & Taylor
Orthotrichum macrocephalum	F.Lara, Garilleti & Mazimpaka
Orthotrichum pallens	Bruch ex Brid.
Orthotrichum philibertii	Venturi
Orthotrichum pumilum	Sw. ex anon.
Orthotrichum rupestre	Schleich. ex Schwägr.
Orthotrichum schimperi	Hammar
Orthotrichum speciosum	Nees
Orthotrichum striatum	Hedw.
Orthotrichum tenellum	Bruch ex Brid.
Orthotrichum tortidontium	F.Lara, Garilleti & Mazimpaka
Ptychostomum capillare	(Hedw.) Holyoak & N.Pedersen
Syntrichia laevipila	Brid.
Syntrichia latifolia	(Bruch ex Hartm.) Huebener
Syntrichia minor	(Bizot) M.T.Gallego, J.Guerra, M.J.Cano, Ros & Sánchez-Moya
Syntrichia papillosa	(Wilson) Jur.
Syntrichia papillosissima	(Copp.) Loeske
Syntrichia princeps	(De Not.) Mitt.
Syntrichia ruralis	(Hedw.) F.Weber & D.Mohr
Syntrichia subpapillosissima	(Bizot & R.B.Pierrot ex W.A.Kramer) M.T.Gallego & J.Guerra
Syntrichia virescens	(De Not.) Ochyra
Tortella humilis	(Hedw.) Jenn.

Continued on next page

Table D2 – *Continued from previous page*

Species	**Author**
Tortella inflexa	(Bruch) Broth.
Tortella tortuosa	(Hedw.) Limpr.
Tortula muralis	Hedw.
Tortula subulata	Hedw.
Zygodon catarinoi	C.Garcia, F.Lara, Sérgio & Sim-Sim
Zygodon conoideus	(Dicks.) Hook. & Taylor
Zygodon rupestris	Schimp. ex Lorentz

Table D3: Coefficients, standard errors, p and t values of all the relationships analyzed

Endogenous variable	Exogenous variable	Std. coef.	Coef.	Std. Error	t value	Pr(>|t|)
Locality richness	Annual Mean Temperature	0.22	0.05	0.01	3.683	>0.001
Locality richness	Temperature seasonality	-0.02	0.00	0.00	-0.276	0.783
Locality richness	Annual precipitation	0.02	0.00	0.00	0.268	0.788
Locality richness	Slope	0.11	0.04	0.02	2.290	0.022
Locality richness	Dummy variable: Forest history, forested	-0.07	-0.70	0.55	-1.286	0.199
Locality richness	Dummy variable: Forest history, degraded	0.12	1.59	0.74	2.149	0.032
Locality richness	Forest percentage	-0.10	-0.03	0.01	-2.289	0.023
Locality richness	Canopy cover	0.04	0.01	0.01	0.708	0.479
Locality richness	Tree density	0.03	0.00	0.00	0.526	0.599
Locality richness	Bark roughness	0.19	0.11	0.03	3.510	>0.001
Locality richness	Diameter	-0.28	-0.15	0.03	-4.589	>0.001
Locality richness	Bryophyte cover	0.26	0.05	0.01	5.748	>0.001
Stand richness	Annual Mean Temperature	-0.03	-0.01	0.03	-0.206	0.838
Stand richness	Temperature seasonality	0.16	0.00	0.00	1.049	0.301
Stand richness	Annual precipitation	0.02	0.00	0.01	0.169	0.867
Stand richness	Slope	-0.03	-0.01	0.01	-0.563	0.574
Stand richness	Dummy variable: Forest history, forested	0.14	1.29	1.04	1.241	0.223
Stand richness	Dummy variable: Forest history, degraded	-0.12	-1.36	1.35	-1.012	0.318
Stand richness	Forest percentage	-0.16	-0.04	0.03	-1.497	0.143
Stand richness	Canopy cover	0.11	0.02	0.03	0.800	0.424
Stand richness	Tree density	-0.17	0.00	0.00	-3.421	0.001
Stand richness	Bark roughness	0.05	0.02	0.01	1.845	0.066
Stand richness	Canopy depth	0.07	0.27	0.08	3.205	0.001
Stand richness	Diameter	-0.11	-0.05	0.01	-3.403	0.001
Stand richness	Transmitted light	-0.02	-0.04	0.04	-1.097	0.273
Stand richness	Locality richness	0.71	0.61	0.09	7.099	>0.001
Sample richness	Dummy variable: Forest history, forested	-0.04	-0.22	0.27	-0.819	0.418
Sample richness	Dummy variable: Forest history, degraded	-0.11	-0.81	0.34	-2.369	0.023
Sample richness	Forest percentage	0.08	0.01	0.01	1.991	0.054
Sample richness	Canopy cover	0.07	0.01	0.01	1.772	0.077
Sample richness	Tree density	0.05	0.00	0.00	1.218	0.224
Sample richness	Bark roughness	0.06	0.02	0.01	1.363	0.174
Sample richness	Canopy depth	0.00	0.01	0.09	0.074	0.941
Sample richness	Diameter	0.06	0.02	0.02	0.880	0.379
Sample richness	Transmitted light	0.02	0.02	0.04	0.589	0.556
Sample richness	Bryophyte cover	0.53	0.05	0.00	14.491	>0.001
Sample richness	Locality richness	0.22	0.12	0.03	3.788	0.001
Sample richness	Stand richnes	0.19	0.12	0.03	3.501	0.001
Bryophyte cover	Dummy variable: Forest history, forested	0.08	4.91	6.39	0.768	0.447
Bryophyte cover	Dummy variable:Forest history, degraded	0.19	14.68	8.08	1.817	0.077
Bryophyte cover	Forest percentage	-0.17	-0.30	0.15	-1.983	0.054
Bryophyte cover	Canopy cover	0.22	0.29	0.09	3.310	0.001
Bryophyte cover	Tree density	-0.07	-0.01	0.01	-0.926	0.357
Bryophyte cover	Bark roughness	0.10	0.31	0.20	1.555	0.121
Bryophyte cover	Canopy depth	0.02	0.40	1.13	0.356	0.722
Bryophyte cover	Diameter	0.27	0.82	0.20	4.125	>0.001
Bryophyte cover	Transmitted light	-0.06	-0.77	0.50	-1.542	0.124

Table D4: Pearson correlations between quantitative exogenous variables

	Slope	Forest percentage	Canopy cover	Tree density	Bark roughness	Diameter	Canopy depth	Transmitted light	Annual Mean Temperature	Temperature seasonality	Annual precipitation
Slope	1.00										
Forest percentage	-0.02	1.00									
Canopy cover	0.17	0.13	1.00								
Tree density	0.20	0.05	0.56	1.00							
Bark roughness	-0.14	-0.08	-0.15	-0.21	1.00						
Diameter	-0.25	-0.15	-0.36	-0.37	0.65	1.00					
Canopy depth	-0.22	-0.03	-0.23	-0.24	0.38	0.47	1.00				
Transmitted light	0.08	0.00	0.09	0.09	0.02	-0.08	-0.16	1.00			
Annual Mean Temperature	-0.14	-0.38	-0.19	-0.24	0.11	0.31	0.18	0.07	1.00		
Temperature seasonality	-0.13	-0.22	0.10	0.15	0.09	0.05	0.09	0.01	0.56	1.00	
Annual precipitation	0.35	0.00	0.05	0.01	-0.16	-0.11	-0.16	0.06	-0.34	-0.69	1.00

Figure D1: Figure depicting all the relationships tested in the a priori model including the correlations among the exogenous variables

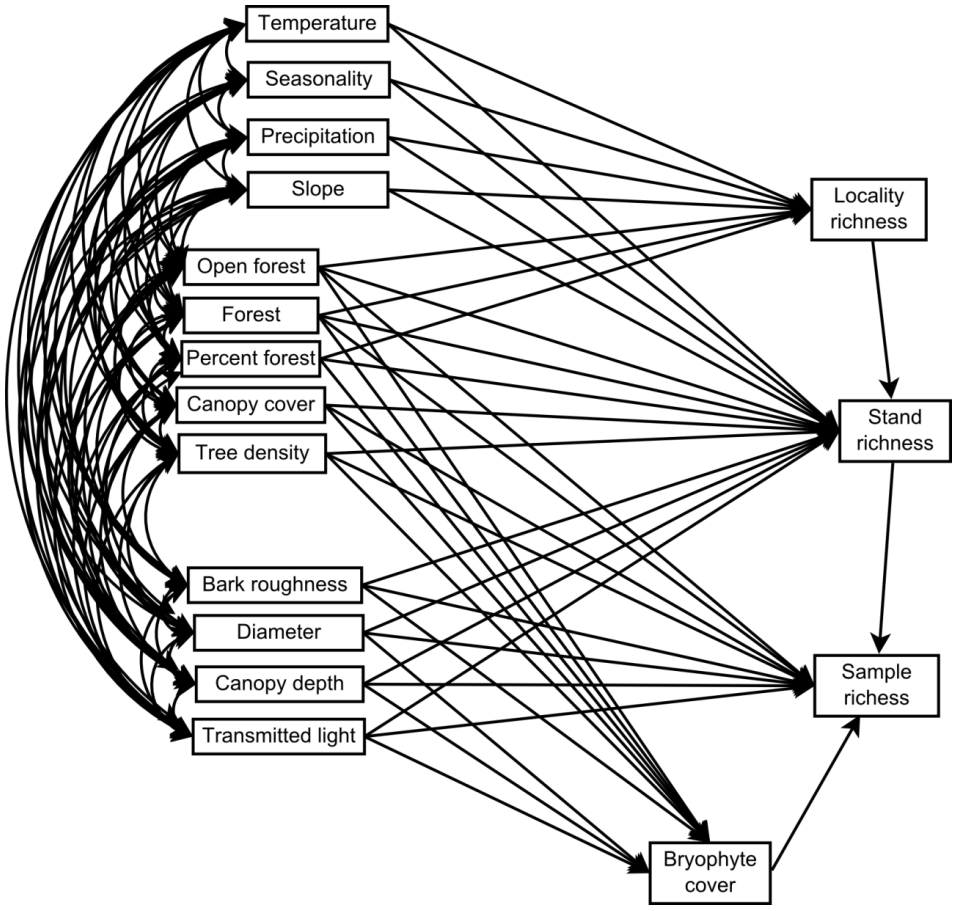


Figure D2: Scheme of the survey design in a stand. Grey area represents the stand area delimited by a circle that includes the six trees placed closer to the center of the stand. d is the diameter of the stand and the distance to the sixth tree. All environmental measurements at this scale are based on the circular plot. Green trees represent trees that were colonized by bryophytes and a star in a tree identifies the sampled trees. Dotted lines divide the stand into four sectors of 45 degrees. Numbers indicate the four trees in which micro-scale environmental characteristics where measured

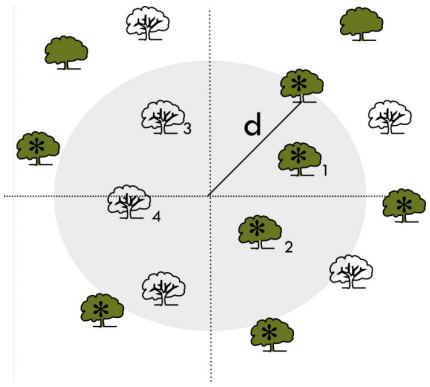
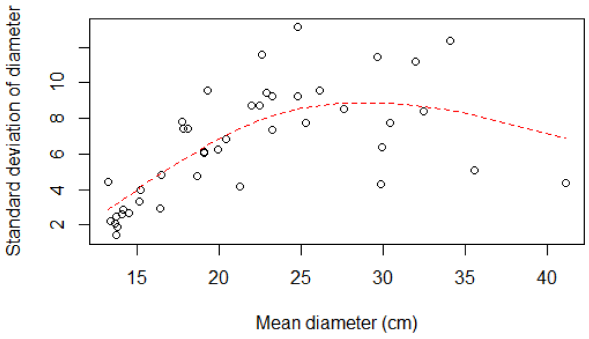


Figure D3: Scatter plot of the average diameter vs. the standard deviation of the diameter at the forest scale



Anexo D.1 **Documented R code for performing the analysis**

We first visually analyzed histograms of the endogenous variables to check for deviation from normality.We tryed several transformations in order to minimize kurtosis and heavy tail effects (square root, box-cox and logaritmic). The transformations only produced slight improvements in the distribution so we kept untransformed endogenous variables for the analysis.

Then visually checked the bivariate plots between endogenous and exogenous variables to identify curvilinear relationships.No curvilinear relationship was identified.

Random structure selection

The analysis workflow is based on the recomendations of Zuur et al [1]. The model selection strategy is a top-down one. First, we specify a model with all the explanatory variables that are considered relevant, the "beyond optimal" model. Second, using the specification of the "beyond optimal" model we compare models with different random structures. Note that to be able to compare models REML (Restricted Maximum Likelihood) is used instead of ML (Maximum likelihood)

Below is the list of variable names used in the analysis (see Table 1 for a complete description):

- rch.loc = locality richness
- ibe_biof1 = Annual mean temperature
- ibe_biof4 = Continentality
- ibe_biof12 = Anual mean precipitation
- slope = Slope
- Forest = Forest history, dummy variable, forested in 1960
- Open.forest = Forest history, dummy variable, strongly degraded in 1960
- perc.forest = Percentage of forest
- cnpy.cover = Canopy cover
- dnsity..tree.ha. = Tree density
- bark.rough = Bark roughness
- diameter = Diameter
- trans.light = Transmitted light
- cnpy.depth = Canopy depth

Prepare the database, specify which variables are factors

```
library(nlme,lme4)
SEM.sin.NA <- read.csv("SEM tabla base rev.csv", sep=";", dec=",")
```

Prepare the database, specify which variables are factors

```
SEM.sin.NA<-SEM.sin.NA[complete.cases(SEM.sin.NA),]
SEM.sin.NA$Forest<-factor(SEM.sin.NA$Forest)
```

[1] Zuur, A., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M. (2009) Mixed effects models and extensions in ecology with R. Springer. New York

```
SEM.sin.NA$Open.forest<−factor(SEM.sin.NA$Open.forest)
SEM.sin.NA$locality<−factor(SEM.sin.NA$locality)
```

Center all the variables except the factors

```
dt <− sapply(SEM.sin.NA,is.factor)
dt2<−which(dt==TRUE)
cent<−SEM.sin.NA[,−dt2]
scaled.data<−as.data.frame(scale(cent))
scaled.data<−cbind(scaled.data, SEM.sin.NA[,dt2])
attach(scaled.data)
attach(SEM.sin.NA)
```

Locality richness

No random structure!

Stand richness

With random structure!

Define the formula that includes all the hypothezised relationships

```
f2<− formula(rch.stand~
rch.loc+
ibe_biof1+ibe_biof4+ibe_biof12+ #climatic variables
slope+ #topographic variables
Forest+Open.forest+perc.forest+ #forest management variables
cnpy.cover+dnsity..tree.ha.+ #forest structure variables
bark.rough+diameter+trans.light+cnpy.depth) #tree characteristics variables
```

Set control parameters for the lme model

```
lmc <− lmeControl(niterEM = 50000, msMaxIter = 50000)
```

Fit possible random structure combinations

```
# Model without random structure at all:
lme.bu0 <− gls(f2)
# Model with random intercept for locality:
lme.bu1 <− lme(f2, random = ~1 | locality)
# Models with random slope for locality:
lme.bu2 <− lme(f2, random = ~bark.rough | locality,control=lmc)
lme.bu3 <− lme(f2, random = ~trans.light | locality,control=lmc)
lme.bu4 <− lme(f2, random = ~cnpy.depth | locality,control=lmc)
lme.bu5 <− lme(f2, random = ~diameter | locality,control=lmc)
lme.bu6 <− lme(f2, random = ~bryo.cover | locality,control=lmc)
```

```
lme.bu7 <− lme(f2, random = ~cnpy.cover | locality,control=lmc)
lme.bu8 <− lme(f2, random = ~dnsity..tree.ha. | locality,control=lmc)
```

Compare the obtained models

```
aov.stn<−anova(lme.bu0, lme.bu1,lme.bu2,lme.bu3,lme.bu4,
 lme.bu5,lme.bu6,lme.bu7,lme.bu8)
```

Select the one with the smallest AIC value

```
aov.stn[which(aov.stn$AIC==min(aov.stn$AIC)),]
```

```
Model df  AIC  BIC logLik Test L.Ratio p-value
lme.bu7     8 19 2131 2209  -1046
```

Sample richness

With random structure!

Define the formula that includes all the hypothezised relationships

```
f3<−formula(rch.sample~rch.loc+
cnpy.cover+dnsity..tree.ha.+#forest structure variables
bark.rough+diameter+cnpy.depth+trans.light+#tree characteristics variables
rch.stand+# stand richness
bryo.cover)#bryophyte cover
```

Select the structure of the random effects

```
# Model without random structure at all:
lme.bu0 <− gls(f3)
# Model with random intercept for locality:
lme.bu1 <− lme(f3, random = ~1 | locality)
#Model with random intercept for stand:
lme.bu2 <− lme(f3, random = ~1 | stand)
#Model with random intercept for locality and stand:
lme.bu3 <− lme(f3, random = ~1 | locality/stand)
#Models with random slope for locality and stand:
lme.bu4 <− lme(f3, random = ~bark.rough | locality/stand)
lme.bu5 <− lme(f3, random = ~trans.light | locality/stand,control=lmc)
lme.bu6 <− lme(f3, random = ~cnpy.depth | locality/stand,control=lmc)
lme.bu7 <− lme(f3, random = ~diameter | locality/stand)
lme.bu8 <− lme(f3, random = ~bryo.cover | locality,control=lmc)
lme.bu9 <− lme(f3, random = ~cnpy.cover | locality,control=lmc)
lme.bu10 <− lme(f3, random = ~dnsity..tree.ha. | locality,control=lmc)
```

Compare the obtained models.

```
aov.smp<−anova(lme.bu0, lme.bu1, lme.bu2,lme.bu3,lme.bu4,lme.bu5,lme.bu6,lme.bu7,
    lme.bu8,lme.bu9,lme.bu10)
```

Select the model with the smallest AIC value

```
aov.smp[which(aov.smp$AIC==min(aov.smp$AIC)),]
```

	Model	df	AIC	BIC	logLik
lme.bu8	9	14	972.9	1031	-472.5

Bryophyte cover

With random structure!**

Define the formula that includes all the hypothezised relationships

```
f4<− formula(bryo.cover~
Forest+Open.forest+perc.forest+#forest management variables
cnpy.cover+dnsity..tree.ha.+#forest structure variables
bark.rough+diameter+cnpy.depth+trans.light#tree characteristics variables
)
```

```
#Model without random structure at all:
lme.bu0 <− gls(f4)
#Model with random intercept for locality:
lme.bu1 <− lme(f4, random = ~1 | locality)
#Model with random intercept for stand:
lme.bu2 <− lme(f4, random = ~1 | stand)
 #Model with random intercept for locality and stand:
lme.bu3 <− lme(f4, random = ~1 | locality/stand)
## Models with random slope for locality and stand
lme.bu4 <− lme(f4, random = ~bark.rough | locality/stand,control=lmc)
lme.bu5 <− lme(f4, random = ~trans.light | locality/stand,control=lmc)
lme.bu6 <− lme(f4, random = ~cnpy.depth | locality/stand,control=lmc)
lme.bu7 <− lme(f4, random = ~diameter | locality/stand,,control=lmc)
lme.bu8 <− lme(f4, random = ~cnpy.cover | locality,control=lmc)
lme.bu9 <− lme(f4, random = ~dnsity..tree.ha. | locality,control=lmc)
```

Compare the obtained models.

```
aov.cov<−anova(lme.bu0, lme.bu1, lme.bu2,lme.bu3,lme.bu4,lme.bu5,lme.bu6,lme.bu7,
    lme.bu8,lme.bu9)
```

Select the one with the lowest AIC value.

```
aov.cov[which(aov.cov$AIC==min(aov.cov$AIC)),]
```

	Model	df	AIC	BIC	logLik
lme.bu7	8	17	4380	4450	-2173

Model Evaluation

To evaluate model performance we conduct a d-separation test based on Shipley (2000a,b,2009)[1]

Graphically express the model

Express the model as a graphic picturing the relationships among variables. See Fig S1 in the appendix section.

Make the list of conditionally independent claims

First make a list of the variables that do not have an arrow between them

- rch.loc - cnpy.cover
- rch.loc - dnsity..tree.ha.
- rch.loc - bark.rough
- rch.loc - diameter
- rch.loc - cnpy.depth
- rch.loc - trans.light
- rch.loc - rch.sample
- rch.loc - bryo.cover
- rch.stand - bryo.cover
- rch.sample - ibe_biof1
- rch.sample - ibe_biof4
- rch.sample - ibe_biof12
- rch.sample - slope
- bryo.cover - ibe_biof1
- bryo.cover - ibe_biof4
- bryo.cover - ibe_biof12
- bryo.cover - slope

And then for each of the k pairs of variables (X_i, X_j), list the set of other variables, {Z} in the graph that are direct causes of either X_i or X_j. The pair of variables (X_i, X_j) along with its conditioning set {Z} define an independence claim, and the full set of the k independence claims defines the basis set BU.

[1] Shipley, B. (2000a) A New Inferential Test for Path Models Based on Directed Acyclic Graphs. Structural Equation Modeling: A Multidisciplinary Journal, 7, 206-218; Shipley, B. (2000b) Cause and Correlation in Biology: A User's Guide to Path Analysis, Structural Equations and Causal Inference. Oxford University Press, Oxford;Shipley, B. (2009) Confirmatory path analysis in a generalized multilevel context. Ecology, 90, 363-368.

Claim		d-separation claim
F1	(rch.loc - cnpy.cover)	{ibe_biof1, ibe_biof4, ibe_biof12, slope, Open.forest, Forest, perc.forest}
F2	(rch.loc - dnsity..tree.ha.)	{ibe_biof1, ibe_biof4, ibe_biof12, slope, Open.forest,Forest, perc.forest}
F3	(rch.loc - bark.rough)	{ibe_biof1, ibe_biof4, ibe_biof12, slope, Open.forest, Forest, perc.forest }
F4	(rch.loc - diameter)	{ibe_biof1, ibe_biof4, ibe_biof12, slope, Open.forest,Forest, perc.forest }
F5	(rch.loc - cnpy.depth)	{ibe_biof1, ibe_biof4, ibe_biof12, slope, Open.forest, Forest, perc.forest }
F6	(rch.loc - trans.light)	{ibe_biof1, ibe_biof4, ibe_biof12, slope, Open.forest, Forest, perc.forest }
F7	(rch.loc - rch.sample)	{ibe_biof1, ibe_biof4, ibe_biof12, slope, Open.forest, Forest, perc.forest, cnpy.cover, dnsity..tree.ha., bark.rough, diameter, cnpy.depth,trans.light,rch.stand}
F8	(rch.loc - bryo.cover)	{ibe_biof1, ibe_biof4, ibe_biof12, slope, Open.forest, Forest, perc.forest, cnpy.cover, dnsity..tree.ha., bark.rough, diameter, cnpy.depth,trans.light}
F9	(rch.stand - bryo.cover)	{ibe_biof1, ibe_biof4, ibe_biof12, slope, Open.forest, Forest, perc.forest, cnpy.cover,dnsity..tree.ha., bark.rough, diameter, cnpy.depth,trans.light,rch.loc}
F10	(rch.sample - ibe_biof1)	{Open.forest, Forest, perc.forest, cnpy.cover, dnsity..tree.ha., bark.rough, diameter, cnpy.depth,trans.light, bryo.cover, rch.stand}
F11	(rch.sample - ibe_biof4)	{Open.forest, Forest, perc.forest, cnpy.cover,dnsity..tree.ha., bark.rough, diameter, cnpy.depth, trans.light, bryo.cover, rch.stand}
F12	(rch.sample - ibe_biof12)	{Open.forest,Forest, perc.forest, cnpy.cover, dnsity..tree.ha., bark.rough, diameter, cnpy.depth, trans.light, bryo.cover, rch.stand}
F13	(rch.sample - slope)	{Open.forest, Forest, perc.forest, cnpy.cover, dnsity..tree.ha., bark.rough, diameter, cnpy.depth, trans.light, bryo.cover, rch.stand}
F14	(bryo.cover - ibe_biof1)	{Open.forest, Forest, perc.forest, cnpy.cover, dnsity..tree.ha., bark.rough, diameter, cnpy.depth, trans.light}
F15	(bryo.cover - ibe_biof4)	{Open.forest, Forest, perc.forest, cnpy.cover, dnsity..tree.ha., bark.rough, diameter, cnpy.depth, trans.light}
F16	(bryo.cover - ibe_biof12)	{Open.forest, Forest, perc.forest, cnpy.cover, dnsity..tree.ha., bark.rough, diameter, cnpy.depth, trans.light}
F17	(bryo.cover - slope)	{Open.forest, Forest, perc.forest,cnpy.cover, dnsity..tree.ha., bark.rough, diameter, cnpy.depth, trans.light}

Calculate the probability of each claim to be independent

For each element in this basis set, obtain the probability, p_k, that the pair (X_i, X_j) is statistically independent conditional on the variables Z.

Previous steps

Set control parameters for the lme model

```
1 lmc <− lmeControl(niterEM = 100000, msMaxIter = 100000)
```

Create a function to run several linear regression lm models at a time

```
x.lm <− function(formula, data, ...)
  {
    Call <− match.call(expand.dots = TRUE)
    Call[[1]] <− as.name("lm")
    Call$formula <− as.formula(terms(formula))
    eval(Call)
  }
```

Create a function to run several lme models at a time

```
lme.fun <− function(formula,random,test.data)
{ form <− as.formula(formula)
    ran.form <− as.formula(random)
    modell <− do.call(lme, list(fixed=form, random=ran.form, data=test.data))
  summary(modell)$tTable
}
```

Create a set of formulae with all the fixed effects affecting endogenous variables (locality richness, stand richness, sample richness and bryophyte cover) in the "a priori" model

```
f.loc<−formula(rch.loc~
          ibe_biof1+ibe_biof4+ibe_biof12+#climatic variables
          slope+#topographic variables
          Forest+Open.forest+perc.forest)#forest management variables

f.stn <− formula(rch.stand~
          rch.loc+
          ibe_biof1+ibe_biof4+ibe_biof12+#climatic variables
          slope+#topographic variables
          Forest+Open.forest+perc.forest+#forest management variables
          cnpy.cover+dnsity..tree.ha.+#forest structure variables
          bark.rough+diameter+trans.light+cnpy.depth)#tree characteristics variables

f.smp<− formula(rch.sample~
          Forest+Open.forest+perc.forest+#forest management variables
          cnpy.cover+dnsity..tree.ha.+#forest structure variables
          bark.rough+diameter+cnpy.depth+trans.light+#tree  characteristics variables
          bryo.cover+
          rch.stand)

f.cov<− formula(bryo.cover~
          Forest+Open.forest+perc.forest+#man
          cnpy.cover+dnsity..tree.ha.+#str
          bark.rough+diameter+cnpy.depth+trans.light#tree
```

```
25                          )
```

Calculate the probability that the pair is statistically independent for each independent claim

```
1 form.list<−list()
2 lme.1<−list()
3 pk<−c(NA)
```

Claim F1

write the formula for the response + environment for the claim

```
1 f1<−formula(paste(deparse(f.loc,width.cutoff=300L),"+cnpy.cover"))
```

calculate the regression

```
1 lme.bu1 <− lm(f1,data=SEM.sin.NA)
```

save the model

```
1 lme.1[[1]] <− lme.bu1
```

caculate the probability p_k that the pair is statistically independent

```
1 pk[1]<−summary(lme.1[[1]])$coefficients[length(all.vars(f1)),4]
```

The rest of the claims

```
1  f2<− formula(paste(deparse(f.loc,width.cutoff=300L),"+dnsity..tree.ha."))
2          lme.1[[2]] <− lm(f2,data=SEM.sin.NA)
3          pk[2]<−summary(lme.1[[2]])$coefficients[length(all.vars(f2)),4]
4  f3<− formula(paste(deparse(f.loc,width.cutoff=300L),"+bark.rough"))
5          lme.1[[3]] <− lm(f3,data=SEM.sin.NA)
6          pk[3]<−summary(lme.1[[3]])$coefficients[length(all.vars(f3)),4]
7  f4<− formula(paste(deparse(f.loc,width.cutoff=300L),"+diameter"))
8          lme.1[[4]] <− lm(f4,data=SEM.sin.NA)
9          pk[4]<−summary(lme.1[[4]])$coefficients[length(all.vars(f4)),4]
10 f5<− formula(paste(deparse(f.loc,width.cutoff=300L),"+cnpy.depth"))
11         lme.1[[5]] <− lm(f5,data=SEM.sin.NA)
12         pk[5]<−summary(lme.1[[5]])$coefficients[length(all.vars(f5)),4]
13 f6<− formula(paste(deparse(f.loc,width.cutoff=300L),"+trans.light"))
14         lme.1[[6]] <− lm(f6,data=SEM.sin.NA)
15         pk[6]<−summary(lme.1[[6]])$coefficients[length(all.vars(f6)),4]
```

```
f7<− formula(paste(deparse(f.loc,width.cutoff=300L),"+cnpy.cover+dnsity..tree.ha.+bark.rough+diameter+
        cnpy.depth+trans.light+bryo.cover+rch.stand+rch.sample"))
        lme.1[[7]] <− lm(f7,data=SEM.sin.NA)
        pk[7]<−summary(lme.1[[7]])$coefficients[length(all.vars(f7)),4]
f8<− formula(paste(deparse(f.loc,width.cutoff=300L),"+cnpy.cover+dnsity..tree.ha.+bark.rough+diameter+cnpy.depth+trans.light+bryo.cover"))
        lme.1[[8]] <− lm(f8,data=SEM.sin.NA)
        pk[8]<−summary(lme.1[[8]])$coefficients[length(all.vars(f8)),4]
f9<− formula(paste(deparse(f.stn,width.cutoff=300L),"+bryo.cover"))
        lme.1[[9]] <− lme(f9,random=~cnpy.cover|locality,method="REML",data=
            SEM.sin.NA)
        pk[9]<−summary(lme.1[[9]])$tTable[length(all.vars(f9)),5]
f10<− formula(paste(deparse(f.smp,width.cutoff=300L),"+ibe_biof1"))
        lme.1[[10]] <− lme(f10,random=~ bryo.cover | locality,method="REML")
    pk[10]<−summary(lme.1[[10]])$tTable[length(all.vars(f10)),5]
f11<− formula(paste(deparse(f.smp,width.cutoff=300L),"+ibe_biof4"))
        lme.1[[11]] <− lme(f11,random=~ bryo.cover | locality,method="REML",data=
            SEM.sin.NA)
        pk[11]<−summary(lme.1[[11]])$tTable[length(all.vars(f11)),5]
f12<− formula(paste(deparse(f.smp,width.cutoff=300L),"+ibe_biof12"))
        lme.1[[12]] <− lme(f12,random=~ bryo.cover | locality,method="REML",data=
            SEM.sin.NA)
        pk[12]<−summary(lme.1[[12]])$tTable[length(all.vars(f12)),5]
f13<− formula(paste(deparse(f.smp,width.cutoff=300L),"+slope"))
        lme.1[[13]] <− lme(f13,random=~ bryo.cover | locality,method="REML",data=
            SEM.sin.NA)
        pk[13]<−summary(lme.1[[13]])$tTable[length(all.vars(f13)),5]
f14<− formula(paste(deparse(f.cov,width.cutoff=300L),"+ibe_biof1"))
        lme.1[[14]] <− lme(f14,random=~ bark.rough |locality,method="REML",data=
            SEM.sin.NA)
        pk[14]<−summary(lme.1[[14]])$tTable[length(all.vars(f14)),5]
f15<− formula(paste(deparse(f.cov,width.cutoff=300L),"+ibe_biof4"))
        lme.1[[15]] <− lme(f15,random=~ bark.rough |locality/stand,method="REML",
            data=SEM.sin.NA)
        pk[15]<−summary(lme.1[[15]])$tTable[length(all.vars(f15)),5]
f16<− formula(paste(deparse(f.cov,width.cutoff=300L),"+ibe_biof12"))
        lme.1[[16]] <− lme(f16,random=~ bark.rough |locality/stand,method="REML",
            data=SEM.sin.NA)
        pk[16]<−summary(lme.1[[16]])$tTable[length(all.vars(f16)),5]
f17<− formula(paste(deparse(f.cov,width.cutoff=300L),"+slope"))
        lme.1[[17]] <− lme(f17,random=~ bark.rough |locality/stand,method="REML",
            data=SEM.sin.NA)
```

```
49        pk[17]<−summary(lme.1[[17]])$tTable[length(all.vars(f17)),5]
```

Calculate the C statistic

The C statistic combines the 17 probabilities of the independence claims using the equation in Shipley (2000):

$C = -2 \sum_{i=1}^{k} ln(p_i)$

and compare the resulting C value to a chi-squared distribution with 2k degrees of freedom. k being the number of independence claims.

```
1 1−pchisq(−2∗sum(log(pk)),df=2∗(length(pk)))
```

```
[1] 2.367e-09
```

As the C is below the chosen significance level (0.05) we reject the causal model ... we need to modify it to include unexpected relationships (new links)

Model Modification

Add the link of the most significant claim

```
1 namepk<−paste("f",c(1:17),sep="")
2 namepk[pk==min(pk)]
3 cbind(namepk,pk)
```

```
[1] "f8"
```

Repeat the procedure until the model is significant

Step 1

Delete independe claim f8 and add the path between rch.sample and rch.loc repeat the d-separation test

Modify claims f1 to f7 and nd recalculate p_i values

```
1 f1<−formula(paste(deparse(f.loc,width.cutoff=300L),"+bryo.cover+cnpy.cover"))
2 f2<− formula(paste(deparse(f.loc,width.cutoff=300L),"+bryo.cover+dnsity..tree.ha."))
3 f3<− formula(paste(deparse(f.loc,width.cutoff=300L),"+bryo.cover+bark.rough"))
4 f4<− formula(paste(deparse(f.loc,width.cutoff=300L),"+bryo.cover+diameter"))
5 f5<− formula(paste(deparse(f.loc,width.cutoff=300L),"+bryo.cover+cnpy.depth"))
6 f6<− formula(paste(deparse(f.loc,width.cutoff=300L),"+bryo.cover+trans.light"))
7 f7<− formula(paste(deparse(f.loc,width.cutoff=300L),"+cnpy.cover+dnsity..tree.ha.+bark
      .rough+diameter+cnpy.depth+trans.light+bryo.cover+rch.stand+rch.sample"))
8
```

```
list1<−list(f1,f2,f3,f4,f5,f6,f7)
namepk1<−paste("f",c(1:7),sep="")
pk1<−NA

for (i in 1:7){
lme.1<−x.lm(list1[[i]],data=SEM.sin.NA)
pk1[i]<−summary(lme.1)$coefficients[length(all.vars(list1[[i]])),4]}
```

The rest of the claims remain the same

```
pk1<−c(pk1,pk[9:17])
namepk1<−c(namepk1,namepk[9:17])
```

Run the test for the model

```
1−pchisq(−2∗sum(log(pk1)),df=2∗(length(pk1)))
```

```
[1] 8.562e-06
```

As the model doesn't fit we find the link with the minimum p-value

```
namepk1[pk1==min(pk1)]
```

```
[1] "f4"
```

Step 2

Delete statement f4 and add the path between diameter and rch.loc

```
f1<−formula(paste(deparse(f.loc,width.cutoff=300L),"+diameter+bryo.cover+cnpy.cover
    "))
f2<− formula(paste(deparse(f.loc,width.cutoff=300L),"+diameter+bryo.cover+dnsity..
    tree.ha."))
f3<− formula(paste(deparse(f.loc,width.cutoff=300L),"+diameter+bryo.cover+bark.
    rough"))
f5<− formula(paste(deparse(f.loc,width.cutoff=300L),"+diameter+bryo.cover+cnpy.
    depth"))
f6<− formula(paste(deparse(f.loc,width.cutoff=300L),"+diameter+bryo.cover+trans.light
    "))
f7<− formula(paste(deparse(f.loc,width.cutoff=300L),"+cnpy.cover+dnsity..tree.ha.+bark
    .rough+diameter+cnpy.depth+trans.light+bryo.cover+rch.stand+rch.sample"))

list2<−list(f1,f2,f3,f5,f6,f7)
namepk2<−paste("f",c(1:3,5:7),sep="")
pk2<−NA
```

```
11
12 for (i in 1:6){
13 lme.1<−x.lm(list2[[i]],data=SEM.sin.NA)
14 pk2[i]<−summary(lme.1)$coefficients[length(all.vars(list2[[i]])),4]}
```

The rest of the claims remain the same

```
1 pk2<−c(pk2,pk1[8:16])
2 namepk2<−c(namepk2,namepk1[8:16])
```

Run the test for the model

```
1 1−pchisq(−2∗sum(log(pk2)),df=2∗(length(pk2)))
```

```
[1] 0.0005787
```

As the model doesn't fit we find the link with the minimum p-value

```
1 cbind(namepk2,pk2)
2 namepk2[pk2==min(pk2)]
```

```
[1] "f3"
```

Step 3

Delete claim f3 and add the path between bark.rough and rch.loc

Modify claims f1 to f7 and recalculate p_i values

```
1 f1<−formula(paste(deparse(f.loc,width.cutoff=300L),"+bark.rough+diameter+bryo.cover
      +cnpy.cover"))
2 f2<− formula(paste(deparse(f.loc,width.cutoff=300L),"+bark.rough+diameter+bryo.
      cover+dnsity..tree.ha."))
3 f5<− formula(paste(deparse(f.loc,width.cutoff=300L),"+bark.rough+diameter+bryo.
      cover+cnpy.depth"))
4 f6<− formula(paste(deparse(f.loc,width.cutoff=300L),"+bark.rough+diameter+bryo.
      cover+trans.light"))
5 f7<− formula(paste(deparse(f.loc,width.cutoff=300L),"+cnpy.cover+dnsity..tree.ha.+bark
      .rough+diameter+cnpy.depth+trans.light+bryo.cover+rch.stand+rch.sample"))
6
7 list3<−list(f1,f2,f5,f6,f7)
8 namepk3<−paste("f",c(1:2,5:7),sep="")
9 pk3<−NA
10
11 for (i in 1:5){
12 lme.1<−x.lm(list3[[i]],data=SEM.sin.NA)
13 pk3[i]<−summary(lme.1)$coefficients[length(all.vars(list3[[i]])),4]}
```

The rest of the claims remain the same

```
pk3<−c(pk3,pk2[7:15])
namepk3<−c(namepk3,namepk2[7:15])
```

Run the test for the model

```
1−pchisq(−2∗sum(log(pk3)),df=2∗(length(pk3)))
```

```
[1] 0.01699
```

As the model doesn't fit we find the link with the minimum p-value

```
cbind(namepk3,pk3)
namepk3[pk3==min(pk3)]
```

```
[1] "f7"
```

Step 4

Delete statement f7 and add the path between trans.light and rch.loc

Modify claims f1 to f6 and recalculate p_i values

```
f1<−formula(paste(deparse(f.loc,width.cutoff=300L),"+rch.sample+bark.rough+diameter
    +bryo.cover+cnpy.cover"))
f2<− formula(paste(deparse(f.loc,width.cutoff=300L),"+rch.sample+bark.rough+
    diameter+bryo.cover+dnsity..tree.ha."))
f5<− formula(paste(deparse(f.loc,width.cutoff=300L),"+rch.sample+bark.rough+
    diameter+bryo.cover+cnpy.depth"))
f6<− formula(paste(deparse(f.loc,width.cutoff=300L),"+rch.sample+bark.rough+
    diameter+bryo.cover+trans.light"))

list4<−list(f1,f2,f5,f6)
namepk4<−paste("f",c(1:2,5,6),sep="")
pk4<−NA

for (i in 1:4){
lme.1<−x.lm(list4[[i]],data=SEM.sin.NA)
pk4[i]<−summary(lme.1)$coefficients[length(all.vars(list4[[i]])),4]}
```

The rest of the claims remain the same

```
pk4<−c(pk4,pk3[6:14])
namepk4<−c(namepk4,namepk3[6:14])
```

Run the test for the model

```
1 1−pchisq(−2∗sum(log(pk4)),df=2∗(length(pk4)))
```

```
[1] 0.2838
```

The model fits the data!!!

```
1 cbind(namepk4,pk4)
```

```
      namepk4     pk4
[1,]   "f1"       0.7935
[2,]   "f2"       0.7674
[3,]   "f5"       0.0899
[4,]   "f6"       0.0387
[5,]   "f9"       0.0459
[6,]   "f10"      0.4177
[7,]   "f11"      0.4281
[8,]   "f12"      0.8935
[9,]   "f13"      0.9586
[10,]  "f14"      0.3623
[11,]  "f15"      0.1819
[12,]  "f16"      0.6843
[13,]  "f17"      0.5495
```

Model Estimation

```
1 library(nlme)
2 library(pander)
3 library(QuantPsyc)
```

Previous steps

Gemerate a function to standardize coefficients

```
1 lme.beta<−
2   function (MOD)
3   {
4     b <− summary(MOD)$tTable[−1, 1]#extract coefficients
5     b<−b[order(names(b))]
6     n<−attr(MOD$terms,"term.labels")
7     sx <− sapply(MOD$data[match(names(MOD$data),n,nomatch=FALSE)>0], sd)#
          extract predictors and calculate sd
8     sx<−sx[order(names(sx))]
```

```
    n2<−attr(MOD$terms,"variables")[[2]]
    sy <− sapply(MOD$data[names(MOD$data)==n2], sd)#extract y value and calculate
        sd
    beta <− b ∗ sx/sy#apply formula
    return(beta)
  }
```

And a function to calculate R-squared values for lme based on Nakagawa and Schielzeth (2012)[1]. The code comes from sample(Ecology) blog by Jonathan S. Lefcheck

`http://jonlefcheck.net/2013/03/13/r2-for-linear-mixed-effects-models/`

```
rsquared.lme=function(modlist) {
  do.call(rbind,lapply(modlist,function(i) {
    if(class(i)=="lm") {
      Rsquared.mat=data.frame(Class=class(i),Marginal=summary(i)$r.squared,
        Conditional=NA,AIC=AIC(i)) }
      else if(inherits(i,"merMod") | class(i)=="merLmerTest") {
      VarF=var(as.vector(fixef(i) %∗% t(i@pp$X)))
      VarRand=colSums(do.call(rbind,lapply(VarCorr(i),function(j) j[1])))
      VarResid=attr(VarCorr(i),"sc")^2
      Rm=VarF/(VarF+VarRand+VarResid)
      Rc=(VarF+VarRand)/(VarF+VarRand+VarResid)
      Rsquared.mat=data.frame(Class=class(i),Marginal=Rm,Conditional=Rc,
        AIC=AIC(update(i,REML=F))) }
    else if(class(i)=="lme") {
     Fmat=model.matrix(eval(i$call$fixed)[−2],i$data)
      VarF=var(as.vector(fixef(i) %∗% t(Fmat)))
      VarRand=sum(suppressWarnings(as.numeric(VarCorr(i)[rownames(VarCorr(i))!=
        "Residual",1])),na.rm=T)
      VarResid=as.numeric(VarCorr(i)[rownames(VarCorr(i))=="Residual",1])
      Rm=VarF/(VarF+VarRand+VarResid)
      Rc=(VarF+VarRand)/(VarF+VarRand+VarResid)
      Rsquared.mat=data.frame(Class=class(i),Marginal=Rm,Conditional=Rc,
        AIC=AIC(update(i,method="ML")))
    } else { print("Function requires models of class lm, lme, mer, or merMod")
} } ) ) }
```

Model for locality richness

[1]Nakagawa, S. & Schielzeth, H. (2013) A general and simple method for obtaining R^2 from generalized linear mixed-effects models. Methods in Ecology and Evolution, 4, 133-142.

```
f.rloc<−formula(rch.loc~
        ibe_biof1+ibe_biof4+ibe_biof12+#climatic variables
    +slope+#topographic variables
    Forest+Open.forest+perc.forest+#forest management variables
    dnsity..tree.ha.+cnpy.cover+#forest structure variables
    +bark.rough+diameter+#tree characteristics variables
    bryo.cover)
lme.loc.def<− lm(f.rloc,data=SEM.sin.NA)
beta.coef<−as.data.frame(lm.beta(lme.loc.def))[,1]
coef.loc<−as.data.frame(summary(lme.loc.def)[[4]])
coef.loc$beta.coef<−c(NA,beta.coef)
simbol.loc<−ifelse(coef.loc[,4]<0.001,"***",ifelse(coef.loc[, 4]<0.01,"**",ifelse(coef.
    loc[,4]<0.05,"*",ifelse(coef.loc[, 4]<0.1,".","")))
coef.loc$simbol<−simbol.loc
summary(lme.loc.def)$r.squared
```

```
[1] 0.2743
```

```
pandoc.table(coef.loc, style="simple",digits=4,split.tables=300)
```

	Estimate	Std. Error	t value
ibe_biof1	0.0535854377	0.014550006	3.6828465
ibe_biof4	−0.000284194	0.001029906	−0.275942
ibe_biof12	0.0009264319	0.003450435	0.2684971
slope	0.0384604597	0.016794318	2.2900877
Forest1	−0.704040601	0.547474570	−1.285978
Open.forest1	1.5942075318	0.741920415	2.1487581
perc.forest	−0.031761992	0.013873217	−2.289446
dnsity..tree.ha.	0.0004238425	0.000805546	0.5261556
cnpy.cover	0.0085692410	0.012105013	0.7079085
bark.rough	0.1082577499	0.030842936	3.5099690
diameter	−0.148001498	0.032249643	−4.589244
bryo.cover	0.0457197165	0.007954405	5.7477230

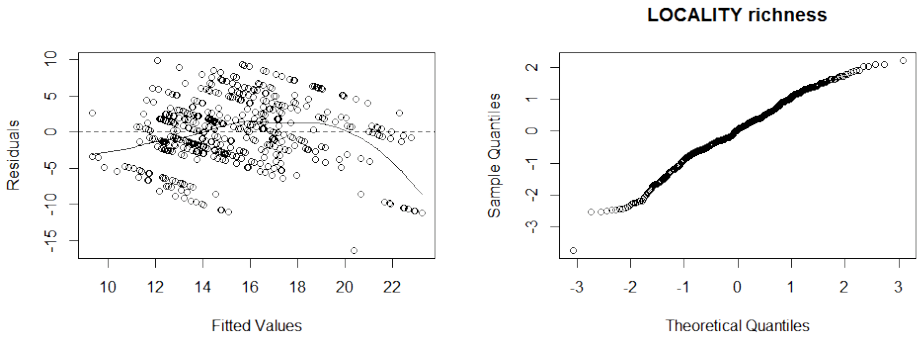
	Pr(>|t|)	beta.coef	simbol
(Intercept)	1.268344e-01	NA	
ibe_biof1	2.579815e-04	0.21838907	***
ibe_biof4	7.827158e-01	−0.0205014	
ibe_biof12	7.884368e-01	0.01713458	
slope	2.246707e-02	0.10562675	*
Forest1	1.990960e-01	−0.0659581	

```
Open.forest1      3.217371e-02  0.11922814      *
perc.forest       2.250456e-02  -0.1043243      *
dnsity..tree.ha.  5.990331e-01  0.02757409
cnpy.cover        4.793598e-01  0.03640502
bark.rough        4.921998e-04  0.19228615    ***
diameter          5.743014e-06  -0.2779667    ***
bryo.cover        1.646840e-08  0.25914539    ***
```

Check residuals and normality

```
plot(fitted(lme.loc.def), residuals(lme.loc.def),
  xlab = "Fitted Values", ylab = "Residuals")
  abline(h=0, lty=2)
  lines(smooth.spline(fitted(lme.loc.def), residuals(lme.loc.def)))
```

```
loc.stdres <- rstandard(lme.loc.def)
qqnorm(loc.stdres,main="LOCALITY richness")
```



Model for stand richness

```
f.rstn <- formula(rch.stand~
      rch.loc+
      ibe_biof1+ibe_biof4+ibe_biof12+#climatic variables
      slope+#topographic variables
      Forest+Open.forest+perc.forest+#forest management variables
      dnsity..tree.ha.+cnpy.cover+#forest structure variables
            bark.rough+diameter+trans.light+cnpy.depth)#tree  characteristics variables

lme.stand.def<-lme(f.rstn,random=~cnpy.cover|locality,data=SEM.sin.NA, method="
      ML")
lme.beta.stand<-lme.beta(lme.stand.def)
```

```
sum.stand<−summary(lme.stand.def)$tTable[−1,]
sum.stand<−sum.stand[order(rownames(sum.stand)),]
mer.stand<−(merge(lme.beta.stand,sum.stand,all=TRUE,by = "row.names"))
simbol.stand<−ifelse(sum.stand[,5]<0.001,"***",ifelse(sum.stand[,      5]<0.01,"**",
    ifelse(sum.stand[,5]<0.05,"*",ifelse(sum.stand[, 5]<0.1,".",""))))
mer.stand$simbol<−simbol.stand
colnames(mer.stand)[2]<−"beta.coef"

rsquared.lme(list(lme.stand.def))
```

```
   Class  Marginal   Conditional   AIC
1   lme    0.1404      0.9725      2055
```

```
pandoc.table(mer.stand, style="simple",digits=4,split.tables=300)
```

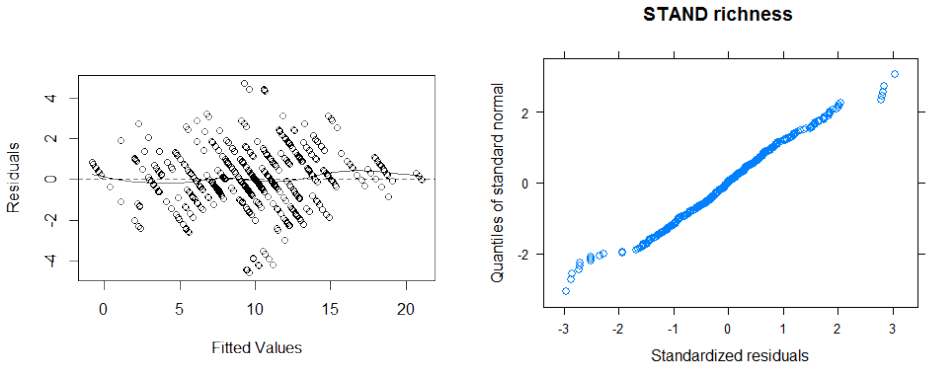
```
        Row.names   beta.coef        Value    Std.Error  DF
       bark.rough  0.04979165  0.024091096 0.0130546913 424
       cnpy.cover  0.10952381  0.022155354 0.0277032490 424
       cnpy.depth  0.07037063  0.271400214 0.0846717442 424
         diameter -0.11058797 -0.050602295 0.0148700002 424
dnsity..tree.ha. -0.16625713 -0.002196204 0.0006419133 424
          Forest1  0.14108966  1.294236910 1.0431493529  35
        ibe_biof1 -0.02584948 -0.005450756 0.0264004372  35
       ibe_biof12  0.02297200  0.001067402 0.0063142397  35
        ibe_biof4  0.16179467  0.001927458 0.0018377169  35
    Open.forest1 -0.11866914 -1.363618828 1.3470326263  35
     perc.forest -0.16190132 -0.042360540 0.0283042189  35
         rch.loc  0.70967033  0.609881861 0.0859114945  35
           slope -0.02622960 -0.008207698 0.0145764603 424
     trans.light -0.02288141 -0.041553372 0.0378644425 424

     t-value      p-value simbol
 1.8453976 6.567679e-02      .
 0.7997385 4.243102e-01
 3.2053221 1.451139e-03     **
-3.4029788 7.299041e-04    ***
-3.4213405 6.835959e-04    ***
 1.2407014 2.229686e-01
-0.2064646 8.376244e-01
 0.1690468 8.667330e-01
 1.0488329 3.014438e-01
-1.0123131 3.183358e-01
```

```
-1.4966157 1.434575e-01
 7.0989553 2.848493e-08    ***
-0.5630790 5.736787e-01
-1.0974246 2.730787e-01
```

Check residuals and normality

```
plot(fitted(lme.stand.def), residuals(lme.stand.def),
  xlab = "Fitted Values", ylab = "Residuals")
  abline(h=0, lty=2)
  lines(smooth.spline(fitted(lme.stand.def), residuals(lme.stand.def)))
qqnorm(lme.stand.def,main="STAND richness")
```



Model for sample richness

```
f.rsmp<− formula(rch.sample~
    Forest+Open.forest+perc.forest+#forest management variables
    cnpy.cover+dnsity..tree.ha.+#forest structure variables
        bark.rough+diameter+cnpy.depth+trans.light#tree characteristics variables
        +rch.loc+rch.stand+bryo.cover)

lme.sample.def<−lme(f.rsmp,random=~diameter|locality,data=SEM.sin.NA,method="
    ML")
lme.beta.sample<−lme.beta(lme.sample.def)
sum.sample<−summary(lme.sample.def)$tTable[−1,]
sum.sample<−sum.sample[order(rownames(sum.sample)),]
mer.sample<−(merge(lme.beta.sample,sum.sample,all=TRUE,by = "row.names"))
simbol.sample<−ifelse(sum.sample[,5]<0.001,"***",ifelse(sum.sample[,5]<0.01,"**",
    ifelse(sum.sample[,5]<0.05,"*",ifelse(sum.sample[,5]<0.1,".",""))))
mer.sample$simbol<−simbol.sample
colnames(mer.sample)[2]<−"beta.coef"
```

```
pandoc.table(mer.sample, style="simple",digits=4,split.tables=300)
rsquared.lme(list(lme.sample.def))
```

```
   Class  Marginal   Conditional  AIC
1   lme    0.5032      0.6855     1940
```

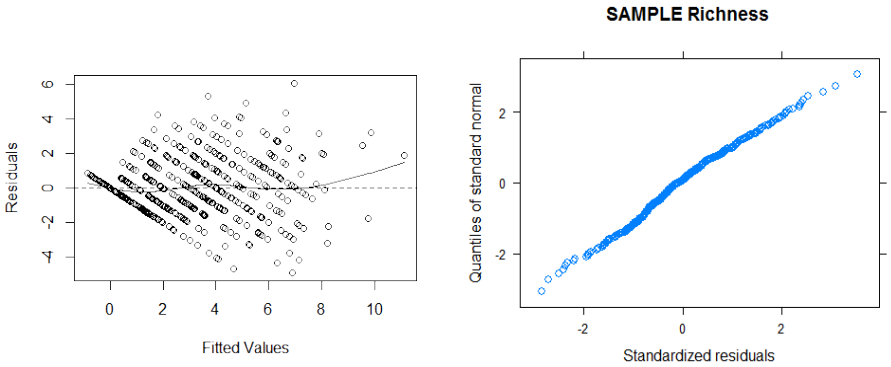
```
pandoc.table(mer.sample, style="simple",digits=4,split.tables=300)
```

```
         Row.names    beta.coef         Value    Std.Error  DF
       bark.rough  0.059824289  0.0182624376 0.0134023204 423
       bryo.cover  0.534444818  0.0511249750 0.0035280089 423
       cnpy.cover  0.073308738  0.0093563619 0.0052789366 423
       cnpy.depth  0.002597612  0.0063208298 0.0850306836 423
         diameter  0.057025398  0.0164631071 0.0187119520 423
dnsity..tree.ha.  0.051667081  0.0004306133 0.0003534417 423
         Forest1 -0.038458593 -0.2225835832 0.2718783566  38
     Open.forest1 -0.111721512 -0.8099777997 0.3419546333  38
      perc.forest  0.080045896  0.0132139088 0.0066366063  38
          rch.loc  0.218023681  0.1182153501 0.0312050672  38
        rch.stand  0.185198527  0.1168472949 0.0333729154 423
      trans.light  0.018870189  0.0216212522 0.0367099769 423
```

```
    t-value      p-value simbol
 1.36263252 1.737234e-01
14.49116960 6.324833e-39    ***
 1.77239520 7.704868e-02      .
 0.07433587 9.407783e-01
 0.87981773 3.794576e-01
 1.21834329 2.237726e-01
-0.81868813 4.180691e-01
-2.36867035 2.303948e-02      *
 1.99106415 5.369955e-02      .
 3.78833827 5.262893e-04    ***
 3.50126124 5.123110e-04    ***
 0.58897482 5.561926e-01
```

Check residuals and normality

```
plot(fitted(lme.sample.def), residuals(lme.sample.def),
  xlab = "Fitted Values", ylab = "Residuals")
  abline(h=0, lty=2)
  lines(smooth.spline(fitted(lme.sample.def), residuals(lme.sample.def)))
qqnorm(lme.sample.def,main="SAMPLE Richness")
```



Model for bryophyte cover

```
f.cov<− formula(bryo.cover~
          Forest+Open.forest+perc.forest+#forest management variables#man
     cnpy.cover+dnsity..tree.ha.+#forest structure variables
          bark.rough+diameter+cnpy.depth+trans.light#tree characteristics variables
)

lme.cover.def<−lme(f.cov,random=~bark.rough|locality/stand,data=SEM.sin.NA,
     method="ML")
lme.beta.cover<−lme.beta(lme.cover.def)
sum.cover<−summary(lme.cover.def)$tTable[−1,]
sum.cover<−sum.cover[order(rownames(sum.cover)),]
mer.cover<−(merge(lme.beta.cover,sum.cover,all=TRUE,by = "row.names"))
simbol.cover<−ifelse(sum.cover[,5]<0.001,"***",ifelse(sum.cover[,5]<0.01,"**",ifelse(
     sum.cover[,5]<0.05,"*",ifelse(sum.cover[,5]<0.1,".","")))))
mer.cover$simbol<−simbol.cover
colnames(mer.cover)[2]<−"beta.coef"
rsquared.lme(list(lme.cover.def))
```

```
  Class Marginal    Conditional  AIC
   1    lme    0.2225       0.4574    4398
```

```
pandoc.table(mer.cover, style="simple",digits=4,split.tables=300)
```

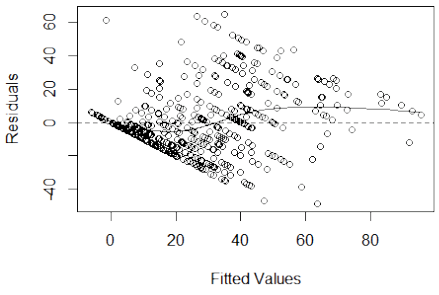
```
     Row.names    beta.coef        Value    Std.Error  DF
    bark.rough   0.09744916   0.310977577 0.199937798 345
    cnpy.cover   0.22098539   0.294838773 0.089075024  80
    cnpy.depth   0.01581002   0.402163024 1.130627544 345
      diameter   0.27051269   0.816396027 0.197931813 345
```

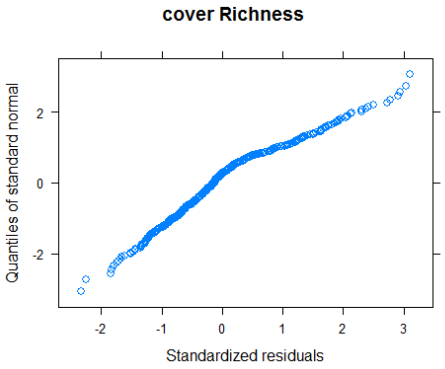
```
dnsity..tree.ha. -0.06934554 -0.006041738 0.006521275  80
         Forest1  0.08113906  4.909072943 6.391493725  39
    Open.forest1  0.19373919 14.683295695 8.082536809  39
     perc.forest -0.17195946 -0.296748180 0.149614932  39
     trans.light -0.06404721 -0.767139947 0.497407170 345

    t-value      p-value simbol
 1.5553716 1.207744e-01
 3.3100050 1.400780e-03     **
 0.3556989 7.222834e-01
 4.1246327 4.657936e-05    ***
-0.9264658 3.569905e-01
 0.7680635 4.470753e-01
 1.8166692 7.695909e-02      .
-1.9834129 5.439378e-02      .
-1.5422776 1.239229e-01
```

Check residuals and normality

```
plot(fitted(lme.cover.def), residuals(lme.cover.def),
  xlab = "Fitted Values", ylab = "Residuals")
  abline(h=0, lty=2)
  lines(smooth.spline(fitted(lme.cover.def), residuals(lme.cover.def)))
qqnorm(lme.cover.def,main="cover Richness")
```





Anexo E **Material complementario al Capítulo 7**

Supplementary material for Chapter 7

Table E1: Species roles and module of each species in each measure type and scale. Ub: Ubiquitous; Wil: Widespread but indicators; Ocp: Occasional but preferential; Ch: Characteristic; ExC: Exclusive and common; ExR: Exclusive and rare. Oth: Other modules

	Binary Forest scale		**Binary Tree scale**		**Abundance Forest scale**		**Abundance Tree scale**	
	module	**role**	**module**	**role**	**module**	**role**	**module**	**role**
Alleniella complanata	1	OcP	1	OcP	1	OcP	1	OcP
Antitrichia californica	3	Ch	4	Ch	4	Ch	Oth	Ch
Antitrichia curtipendula	1	ExC	1	ExC	1	ExC	Oth	Ch
Brachytheciastrum velutinum	4	WiI	7	WiI	2	OcP	Oth	Ch
Bryum argenteum	3	ExR	5	ExR	3	ExR	5	ExR
Ceratodon purpureus	4	OcP	5	OcP	3	OcP	3	OcP
Cryphaea heteromalla	1	ExR	1	ExR	1	ExR	1	ExR
Dialytrichia saxicola	3	OcP	4	OcP	4	ExR	5	ExC
Dicranoweisia cirrata	1	OcP	1	OcP	1	Ch	1	OcP
Dicranum scoparium	1	ExC	1	ExC	1	ExC	1	ExR
Didymodon insulanus	4	ExR	5	ExR	3	OcP	7	OcP
Didymodon vinealis	3	OcP	4	OcP	4	OcP	5	Ch
Ditrichum heteromallum	4	ExR	7	ExR	2	ExR	Oth	ExR
Fabronia pusilla	3	Ch	4	Ch	4	Ch	5	Ch
Frullania dilatata	1	WiI	1	WiI	1	Ch	8	Ch
Frullania microphylla	1	ExR	1	ExR	1	ExR	1	ExR
Frullania tamarisci	1	ExC	1	ExC	1	ExC	1	ExC
Grimmia laevigata	2	OcP	3	OcP	3	OcP	6	OcP
Grimmia lisae	3	Ch	4	Ch	4	Ch	5	WiI
Grimmia pulvinata	3	Ch	5	Ch	3	Ch	7	Ub
Grimmia trichophylla	3	Ch	4	Ch	3	OcP	6	Ub
Habrodon perpusillus	2	OcP	2	OcP	2	OcP	2	OcP
Hedwigia ciliate	3	Ub	6	Ub	3	Ch	6	OcP
Hedwigia stellate	3	Ch	4	Ch	3	OcP	6	OcP
Homalothecium aureum	4	Ch	4	Ch	4	WiI	Oth	Ch
Homalothecium lutescens	2	Ch	7	Ch	6	Ch	Oth	ExC
Homalothecium sericeum	2	WiI	3	WiI	5	WiI	4	Ch
Hypnum andoi	1	ExC	1	ExC	1	ExC	1	Ch

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Table E1 – *Continued from previous page*

	Binary Forest scale		Binary Tree scale		Abundance Forest scale		Abundance Tree scale	
	module	**role**	**module**	**role**	**module**	**role**	**module**	**role**
Hypnum cupressiforme	2	WiI	1	WiI	2	WiI	1	Ch
Isothecium alopecuroides	1	ExR	1	ExR	1	ExR	1	OcP
Isothecium myosuroides	1	ExC	1	ExC	1	ExC	1	OcP
Lejeunea lamacerina	1	ExR	1	ExR	1	ExR	1	ExR
Leptodon smithii	3	ExR	4	ExR	4	ExR	Oth	ExR
Leucodon sciuroides	2	Ch	3	Ch	5	WiI	4	Ch
Metzgeria fruticulosa	1	ExR	1	ExR	1	ExR	8	ExR
Metzgeria furcate	1	ExC	1	ExC	1	ExC	1	OcP
Neckera pumila	1	ExC	1	ExC	1	ExC	1	Ch
Nogopterium gracile	1	OcP	1	OcP	1	OcP	1	OcP
Nyholmiella obtusifolia	2	ExR	2	ExR	3	OcP	Oth	Ch
Orthotrichum acuminatum	2	WiI	6	WiI	3	Ch	6	Ch
Orthotrichum affine	2	WiI	2	WiI	2	Ch	2	Ch
Orthotrichum anomalum	4	ExR	4	ExR	3	ExR	4	ExR
Orthotrichum columbicum	1	ExR	1	ExR	1	ExR	1	OcP
Orthotrichum comosum	3	WiI	6	WiI	3	Ch	6	Ch
Orthotrichum cupulatum	2	ExR	3	ExR	5	ExR	4	ExR
Orthotrichum diaphanum	3	Ch	5	Ch	3	Ch	7	Ch
Orthotrichum ibericum	2	OcP	2	OcP	2	ExC	2	OcP
Orthotrichum lyellii	2	WiI	2	WiI	2	WiI	3	WiI
Orthotrichum macrocephalum	3	OcP	6	OcP	3	ExR	Oth	OcP
Orthotrichum pallens	2	OcP	6	OcP	2	OcP	8	Ub
Orthotrichum philibertii	3	Ch	4	Ch	4	Ch	7	Ch
Orthotrichum pumilum	2	WiI	6	WiI	3	Ch	7	OcP
Orthotrichum rupestre	2	WiI	2	WiI	3	Ch	6	Ch
Orthotrichum schimperi	3	Ch	5	Ch	3	Ch	7	Ch
Orthotrichum speciosum	2	Ch	2	Ch	2	Ch	2	Ch
Orthotrichum stramineum	1	OcP	2	OcP	2	Ch	2	OcP
Orthotrichum striatum	2	Ch	2	Ch	2	Ch	2	Ch
Orthotrichum tenellum	3	Ch	5	Ch	3	Ch	7	Ch
Orthotrichum tortidontium	2	ExR	2	ExR	2	OcP	2	OcP
Orthotrichum vittii	2	Ch	7	Ch	2	OcP	Oth	Ch
Porella obtusata	1	ExR	1	ExR	1	ExR	4	ExR

Continued on next page

Table E1 – *Continued from previous page*

	Binary Forest scale		Binary Tree scale		Abundance Forest scale		Abundance Tree scale	
	module	**role**	**module**	**role**	**module**	**role**	**module**	**role**
Porella platyphylla	2	OcP	3	OcP	2	OcP	4	Ub
Pterigynandrum filiforme	1	Ch	1	Ch	1	Ch	1	Ch
Ptychostomum capillare	3	Ch	4	Ch	4	OcP	5	WiI
Radula complanata	1	ExC	1	ExC	1	Ch	1	Ch
Syntrichia calcicola	3	ExR	3	ExR	2	ExR	2	ExR
Syntrichia laevipila	3	Ch	5	Ch	4	Ch	5	Ch
Syntrichia latifolia	3	OcP	5	OcP	3	OcP	5	Ch
Syntrichia minor	3	OcP	4	OcP	4	OcP	5	Ch
Syntrichia papillosa	3	Ch	5	Ch	3	Ch	7	Ch
Syntrichia papillosissima	2	OcP	2	OcP	3	OcP	7	OcP
Syntrichia princeps	3	OcP	5	OcP	4	Ch	5	Ch
Syntrichia ruralis	4	OcP	5	OcP	3	OcP	5	Ch
Syntrichia subpapillosissima	4	ExR	4	ExR	3	ExR	6	OcP
Syntrichia virescens	3	WiI	3	WiI	5	WiI	4	Ch
Tortella humilis	4	OcP	7	OcP	3	OcP	Oth	OcP
Tortella inclinata	1	ExR	1	ExR	2	ExR	Oth	Ch
Tortella inflexa	4	ExR	6	ExR	3	ExR	2	OcP
Tortula muralis	3	ExR	4	ExR	4	ExR	5	ExR
Tortula subulata	4	ExR	4	ExR	3	ExR	7	OcP
Ulota bruchii	1	ExC	1	ExC	1	ExC	1	Ch
Ulota coarctata	1	ExR	1	ExR	1	ExR	1	OcP
Ulota crispa	1	ExC	1	ExC	1	Ch	1	Ch
Ulota crispula	1	ExC	1	ExC	1	ExC	2	OcP
Zygodon catarinoi	3	Ch	4	Ch	4	Ch	5	Ch
Zygodon conoideus	1	OcP	1	OcP	1	OcP	1	OcP
Zygodon rupestris	3	WiI	3	WiI	4	Ch	4	Ch
Zygodon viridissimus	2	ExR	3	ExR	3	OcP	4	ExR

Table E2: Results of the regression analysis. Numbers indicate unstandardized coefficients. Significance codes: 0.0001> '***'; 0.001>'**'; 0.01>'*'; 0.05>'.' 0.1)

	All modules	**Module 1**	**Module 2**	**Module 3**	**Module 4**
R-squared	0.56	0.62	0.61	0.79	0.94
Commonness	-0.013	-0.01**	-0.007**	-0.011***	-0.005.
Precipitation of Warmest Quarter				-0.001**	
Precipitation of Driest Month				-0.011***	
Precipitation of Coldest Quarter				-0.001*	
Mean Diurnal Range			-0.004.		
Slope	0.001		0.002**	-0.001**	
Forest type (*Q. pyrenaica*)	-0.076		-0.14***		
Forest type (*Q. faginea*)	0.025		0.005		
Bark roughness	0.005		0.008.		
Canopy depth				-0.028**	
Leaf Area Index	0.001				

Table E3: Relative importance of predictor groups for within forest beta diversity

	All modules	**Module 1**	**Module 2**	**Module 3**	**Module 4**
R-squared	56.4	61.9	61.4	79.1	94.5
Commonness	38.6	61.9	11.9	27.9	94.5
Climate	-	-	4.1	23.3	-
Topography	3.5	-	9.9	6.3	-
Habitat characteristics	6.6	-	45.6	-	-
Micro-scale environment	2.9	-	4.5	5.8	-
Joint	4.8	-	-14.8	15.6	-

Table E4: Results of the generalized dissimilarity models. S1, S2, S3 stand for the coefficients fitted to the three I-spline basis functions for each predictor

	All modules			**Module 1**			**Module 2**			**Module 3**			**Module 4**		
	S1	**S2**	**S3**	**S1**	**S2**	**S3**	**S1**	**S2**	**S3**	**S1**	**S2**	**S3**	**S1**	**S2**	**S3**
Distance	0.14	0	0.14	0.12	0.4	0.13	0.09	0	0.11	0.17	0	0	0.21	0.15	0
Commonness	0	0.04	0	0	0	0.07	0	0.10	0	0	0.04	0.6			
Climate axis 1	0.55	0.13	0.37				0.71	0	0				0	0.06	0
Slope				0	0.08	0.29							0.03	0	0.27
Canopy cover	0	0.21	0.03	0.04	0.13	0	0.13	0	0.16				0.77	0	0.16
Forest diameter	0.26	0	0.1				0.13	0.19	0.25	0.19	0	0.08	0.2	0.05	0
Habitat heterogeneity							0.20	0	0.20				0	0	0
Micro-scale heterogeneity							0	0.08	0	0.17	0.02	0	0.07	0	0.09
Canopy depth	0.39	0	0.07	0	0.01	0.17	0	0.01	0	0.30	0.06	0.21			
Bark roughness	0.4	0	0.03	0.4	0	0.08	0.06	0	0	0.03	0.18	0			
Leaf Area Index	0.05	0.36	0	0.04	0		0.20	0	0.37				0.11	0.05	0

Figure E1: Summary of environmental variables

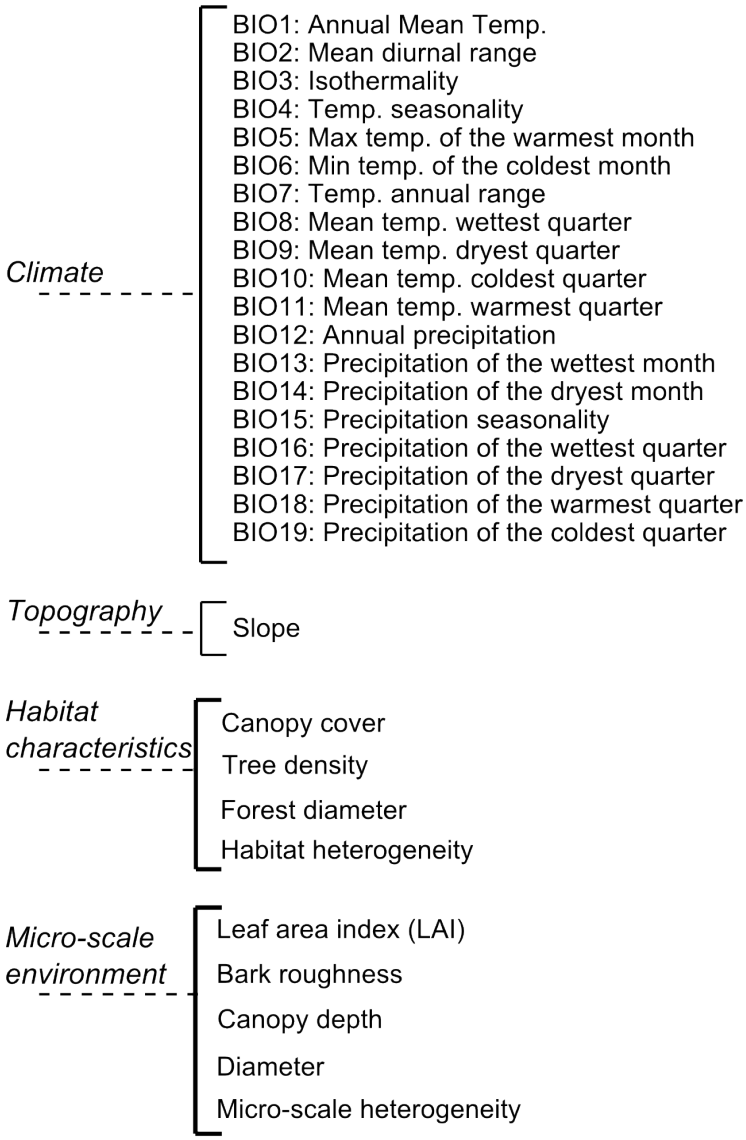


Figure E2: Summary of the results of the network analyses for abundance data. (a) Table relating modules in the network at tree (columns) and forest (rows) scales. Data in the body of the table are the number of trees in each category, for example, module 1 includes 132 trees in module A, 59 trees in module B and so on. For each module at the tree scale (column), the highest figure is circled. (b) Distribution of modules at the forest scale. Circle colors depict the module to which the forest belongs. Circle size indicates the degree of participation of the forest in its module, that is, the density of links that the forest has within the module in relation to the density of links outside the module. (c) Distribution of the modules at the tree scale. Each pie chart represents a forest and pie sectors indicate the percentage of trees belonging to each module in that forest. Pie size is related to the percentage of trees colonized by bryophytes in that forest

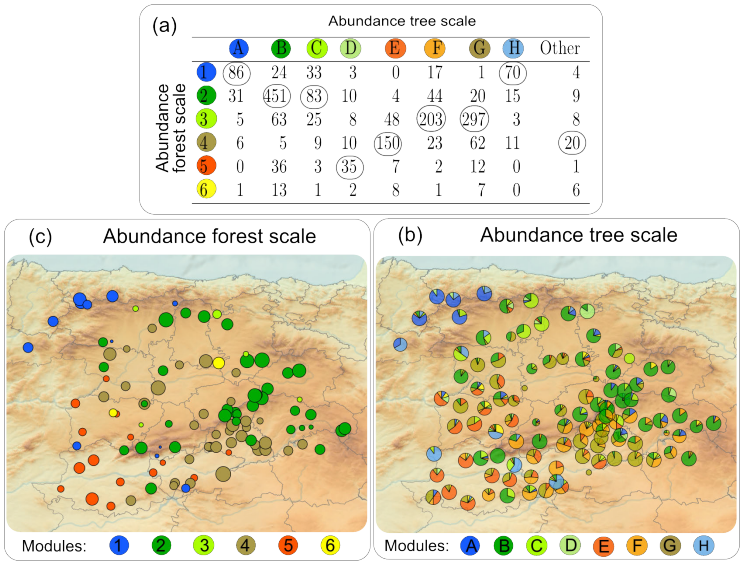
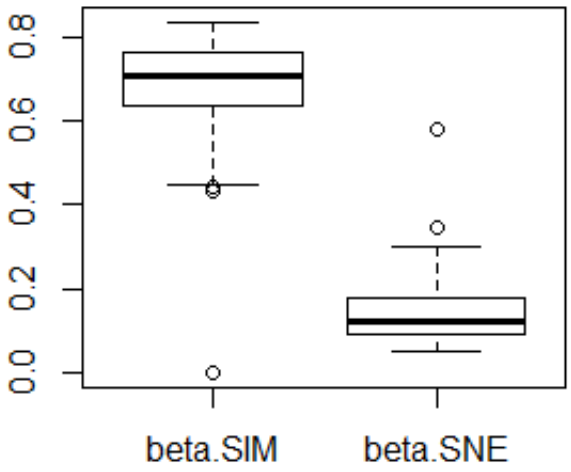


Figure E3: Boxplot of beta similarity and beta nestedness values



Anexo E.1 **Description of the environmental variables**

The environment was characterized according to three groups of predictors (see Fig. E1): i) *Climate* that was measured at the forest scale and included 19 bioclimatic variables extracted from Worldclim (Hijmans *et al.* 2006); ii) *Topography* slope that was visually estimated in each stand during the field campaigns; iii) *Habitat characteristics* that were measured at stand scale (three stands per forest, the values of the variables are averaged per forest) and included three variables estimated in the field: canopy cover that stands for the percentage of forest floor covered by the crowns of the trees, tree density that is an estimate of the number of trees per ha. and forest diameter that is an estimation of the average diameter of the trees of the forest; iv) *Micro-scale environment* that was measured at tree scale (to measure them we selected 4 trees per stand, twelve trees per forest) and included four variables: leaf area index (LAI) that describes the amount of sky covered by the canopy; bark roughness that measures the depth of the furrows of the bark; canopy depth that measures the profundity of the tree crown in meters; and diameter that stands for the diameter at the breast height of the tree. Besides these variables we also calculated the *environmental heterogeneity* both in habitat characteristics and micro-scale environment. For this purpose we first calculated two dissimilarity matrices using Gower distance metric, the first based on the three variables describing habitat characteristics and the second one based on the four variables characterizing the micro-environment. Then we used the fdisp function in FD package (Laliberté *et al.* 2010) to calculate the two measures of habitat heterogeneity. The function calculates the average distance of individual measures in a PcOA space based on a dissimilarity measure as described in Anderson (2006)

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Anexo E.2 **Expanded explantaions on network analysis methods**

Modularity significance

To test whether our networks were more modular than random expectations, we compared the observed modularity values against the distributions of that value for 99 random networks. The probability (*P*) of the observed modularity being higher than random expectations was calculated as the proportion of random networks that were equally or more modular than the observed network, being the observed modularity value also included. To generate the random networks we used the independent swap algorithm as implement in the R package(R Core Team, 2013)picante (Kembel *et al.* 2010). This algorithm maintains species occurrence frequency (or species abundance in the case of weighted networks) and site species richness. We found that the four analysed networks were significantly modular (in all cases *P*= 0.01)

Node participation

In order to define the network species roles we computed two indicators based on the species network participation (Guimera & Amaral, 2005; see also Carstensen et al. 2013). The first indicator (intra-modular connectivity, IAM) is based on the density of intra-modular links.

$$IAM = \frac{K_{in} - \overline{K}_n}{SD_{kn}}$$

where is the number of links connecting the species *i* to sites in its module *n*. and are the average and standard distribution respectively of overall species in the module *n*. Thus, this index is a measure of how well a given species is connected to its module relative to the species from its own module. In other words, *IAM* can be considered as a measure of how representative is a given species within its module.

The second indicator (inter-modular connectivity, *IEM*) is based on the distribution of links between modules.

$$IEM = 1 - \sum_{N}^{n=1} \left(\frac{k_{ni}}{k_i} \right)^2$$

where is the number of links of the species *i* connecting to sites from module *n* and is the total number of links of species *i*. Notice, that this index is equal to one minus the many times rediscovered Simpson's index. Thus, the index will take values of 0 when the species *i* has all its links within a module and will tend to 1 when the species *i* has its links evenly distributed among all modules.

If we plot *IAM* as a function of *IEM* we obtain what Cartensen (2013) has called the l-r space (see Fig. 2a for a species centred graph). This space can be divided into quadrants that delimit the different roles of species or sites in the network. The horizontal line is defined by the median of IAM (Guimerà & Amaral 2005; Carstensen *et al.* 2013). The vertical divisions are a simplified version of the divisions in Guimerà & Amaral (2005) where the two vertical lines represent IEM = 0.1 (species with IEM <0.1 have almost all

their links within their module) and IEM =0.625 (species with IEM < 0.625 have at least half of their links outside their module).

Similarities in species module co-occurrence between networks

We further investigated to what extend the species composition of modules from the tree network were similar to the species composition of the modules from the forest network. To do so, we first compute the degree of co-occurrence into modules for each species pair using Schoener's co-occurrence index (Schoener 1970, see Krasnov *et al.* 2012 for a similar approach). We then explored whether pairwise values of co-ocurrence were correlated between the tree network and the forest network by using Spearman's correlation coefficient. Finally, the significance of the correlation was estimated by comparison of the observed coefficient with the mean of coefficients computed for 9999 randomized null matrices (either for the forest matrix or the tree matrix) generated using the independent swap algorithm (see above). We consider the correlation being significant if it was equal or higher than 99% of null correlations.

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